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Modulating visuomotor adaptation in young healthy adults: Effects of reward and punishment

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ABSTRACT

Recent human motor adaptation/learning studies revealed that punishment accelerates acquisition of motor memory while reward enhances consolidation of motor memory. This study tested the robustness and a possible cause for this potential dissociation. During learning to adapt to an abrupt visual rotation in moving to a visual target, young healthy participants were provided with performance-based monetary reward or punishment. By manipulating the probability of reward or punishment distribution and controlling visual feedback of the cursor while moving to a target, the present study demonstrated that punishment induced faster adaptation than reward in both continuous and non-continuous visual feedback contexts when punishment and reward were distributed in all adaptation trials. However, only reward combined with continuous visual feedback of the cursor resulted in offline consolidation improvement. In contrast, offline consolidation of punishment-induced adaptation memory was inhibited in the continuous visual feedback context. A word-list learning task immediately after the adaptation training reduced this inhibition of punishment-induced adaptation memory, while having no influence on the consolidation of reward-induced adaptation memory. These findings suggest that punishment, compared to reward, induced more efficient explicit process in the adaptation phase, but stronger explicit memory suppressed the consolidation of the punishment-induced motor memory.

Key words: reward, punishment, visuomotor adaptation, savings.

CHAPTER 1. INTRODUCTION

We live in an ever-changing environment. To move flexibly and precisely, we need to adjust motor commands to counteract changes imposed by external perturbations. This process is termed motor adaptation. Different from the motor skill learning paradigm, studies used a motor adaptation paradigm to uncover the processes and factors underlying how one counteracts external perturbations to maintain performance of previously learned movement patterns. This is of significance to our daily living in that any learned movement pattern may be disturbed and we must adapt to new conditions.

Motor adaptation occurs with practice in many movements such as reaching, walking, and eye movement (Shadmehr & Mussa-Ivaldi 1994; Reisman et al. 2005; Wallman & Fuchs 1998). Reaching is one of the most frequently used actions in human daily living. Normal reaching can be disturbed by an external mechanical perturbation on the reaching arm or transformation of visual feedback of the reaching hand. In experimental studies on reaching adaptation, an external mechanical perturbation is often manipulated by introducing a novel force field (Dizio & Lackner 1995), while a visual perturbation is introduced by wearing prism glasses to shift the view of the external world (Martin et al. 1996) or by rotating the visual display of the reaching hand (usually a cursor) in a virtual reality environment like computer monitor (Cheng & Sabes 2007).

When a mechanical or visual perturbation is applied to reaching, it induces kinematic or endpoint movement errors and makes the originally learned reaching stray from its normal trajectory. Participants then need practice to adapt to the perturbation. A critical feature of motor adaptation is that it allows individuals to alter motor commands based on movement errors from prior trials. By altering motor commands, movement error can be reduced from one trial to the next.

The adaptation to a visual perturbation in reaching is termed "visuomotor adaptation." Studies indicate that sensory feedback and motivational feedback influence visuomotor adaptation comparably, but they have different effects on washout, re-adaptation, and generalization (Izawa & Shadmehr 2011; Nikooyan & Ahmed 2015). It is thought that sensory feedback and motivational feedback involve different learning mechanism and neural underpinnings. Visuomotor adaptation driven by sensory feedback is a kind of error-based learning, in which movement errors are detected by sensory systems and the error information is used to update motor commands for subsequent actions (Seidler et al. 2013). Extensive evidence indicates that the cerebellum plays critical roles in error-based motor learning (Seidler et al. 2013; Tseng et al. 2007). In contrast, visuomotor adaptation driven by motivational feedback is a kind of reinforcement learning, in which participants are rewarded or punished in each trial and they must learn the mapping between reward/punishment states and corresponding actions so to maximize future reward or minimize future punishment (Wolpert et al. 2001). Evidence indicates that the basal ganglia and dopamine play a role in reinforcement learning (Dayan & Balleine 2002).

Sensory feedback is manipulated by controlling the continuous (online) or endpoint-only visual feedback of the visual perturbation introduced. In a continuous visual feedback condition, participants see the reaching hand or the cursor from the start to the end of a reaching trial. In an endpoint-only visual feedback condition, participants can only see the reaching hand or the cursor at the end of a reaching trial. The two types of visual feedback provide participants with different sensory error information and influence the visuomotor adaptation process differently.

When continuous visual feedback of the reaching hand or the cursor is provided in the adaptation phase, participants gain sensory prediction errors, which are the differences between the expected movement consequences and the observed movement consequences, and reflect whether the reaching arm moved in the way that the brain thought it would (Miall et al. 2007). Sensory prediction error is thought to be a crucial factor driving visuomotor adaptation (for review see, Shadmehr et al. 2010). The reason that we predict sensory consequence of a movement lies in the unavoidable delay in the conduction of sensory afferent signals from the periphery. The sensory conduction delay causes the perceived body state to always lag in its true state and, thus, induces difficulty in the control of fast movements like reaching and aiming (Wolpert & Flanagan 2001). Human movements are not solely based on current sensory feedback but rather on an integration of sensory feedback and sensory prediction. This integration is thought to be achieved through a forward model that probably resides in the cerebellum and its output can be used in the control of movements in visuomotor adaptation (Tseng, et al. 2007).

When endpoint-only visual feedback of the reaching hand or the cursor is provided in the adaptation phase, participants gain endpoint error, which is also capable of driving participants to adapt to visual perturbation in reaching. Visuomotor adaptation with endpoint-only visual feedback was comparable to adaptation with continuous visual feedback during a reach (Izawa & Shadmehr 2011; Hinder et al. 2008). However, when re-exposed to the non-rotated environment, only participants who received continuous visual feedback of the cursor exhibited clear after-effects, manifested as an increased angular deviation of the cursor moving path (Hinder et al. 2008; Hinder et al. 2010). Moreover, when reaching to new targets, generalization was stronger after the adaptation with continuous visual feedback of the cursor than that after the adaptation with only endpoint visual feedback of the cursor (Hinder et al. 2008; Shabbott & Sainburg 2010). The differences in after-effects and generalization in continuous and endpoint-only feedback conditions indicate that continuous and endpoint-only error information may activate different mechanisms or strategies to attain comparable adaptation performances. In the context of continuous sensory feedback, participants obtain both performance error and sensory prediction error, with the adaptation driven by the interplay of explicit and implicit processes. In contrast, in the context of endpoint-only sensory feedback, participants only gain performance error, with the adaptation primarily driven by explicit process.

The traditional view held is that motor adaptation is an implicit process driven by sensory prediction error. However, a series of recent studies revealed that motivational feedback facilitated motor adaptation, reflecting different mechanisms

may underlie motor adaptation. This study focuses on the effects of motivational feedback, specifically monetary reward and punishment, on visuomotor adaptation.

The learning and execution of movement skills is naturally associated with reward and punishment. For instance, a proper aim and reach for a cup of coffee results in enjoying the coffee but a miscalculated reach results in spilled coffee at best, and burned at worst. Properly driving a rental car results in timely and comfortable transport from one place to another, but poor adaptation to the new car may result in an accident and possible bodily injury. The naturally associated reward and punishment may modulate the learning and execution of movements.

Izawa and Shadmehr (2011) found that sensory feedback and motivational feedback functioned differently in visuomotor adaptation. They hypothesized motor adaptation would become more dependent on reward feedback as the quality of the sensory feedback degraded, i.e., from continuous visual feedback to endpoint-only visual feedback. They designed a rapid aiming movement adaptation study, in which three groups of participants adapted to a cursor rotation when executing rapid aiming movements. The researchers manipulated the type of visual feedback regarding cursor position. In one group the cursor was available throughout the rapid aiming. In another group the cursor was available only at the end of the rapid aiming. In a third group the cursor was unavailable at any point throughout the rapid aiming. All three groups had access to the reward (aiming success indicated by target explosion animation) at the end of their aiming. In the adaptation phase, the three groups

experienced cursor rotation that was rotated around the center at the start position and increased by 1° every 40 trials until it reached 8°. They analyzed the adaptation process and generalization to seven-target rapid aiming movements.

They (Izawa and Shadmehr, 2011) found that all three groups learned to adapt to the gradual cursor rotation after a long period of practice but the trial-to-trial variability, generalization pattern, and perceived sensory consequence (the estimated position of the cursor indicated by pointing of the non-aiming hand on the monitor when both the cursor and the target were not displayed) differed between the two sensory error groups and the reward-only group. The sensory error groups showed lower variability of aiming direction, a wide pattern of generalization, and a significant change in the perceived position of the aiming hand. The reward error group showed higher variability of aiming direction, a narrow pattern of generalization, and no change in the perceived position of the aiming hand. The researchers concluded that both sensory prediction error and reward feedback can drive visuomotor adaptation, but only sensory prediction errors produce changes in the prediction of sensory consequence of visuomotor adaptation.

Nikooyan and Ahmed (2015) used a visuomotor adaptation task to explore the effects of sensory feedback and motivational feedback on motor adaptation. Young healthy participants were rewarded by using a linear or a cubic scoring system when they learned to adapt to an abrupt 30° counterclockwise (CCW) visual rotation of a cursor in doing fast reaching movements. They demonstrated that reward feedback

alone drove adaptation to the abrupt visual rotation, with the combination of reward and sensory feedback accelerating the visuomotor adaptation.

In another visuomotor adaptation study, Galea and colleagues (2015) further demonstrated that monetary punishment and reward had dissociable effects on visuomotor adaptation and retention of the adaptation memory. Specifically, the researchers provided young healthy adults with monetary reward or punishment according to endpoint performance error while learning to adapt to an abrupt 30° CCW cursor rotation. They found that the punishment group exhibited faster adaptation when visual feedback of the cursor was provided, but the reward group exhibited better retention of the acquired adaptation when visual feedback of the cursor was not provided.

In contrast to previous findings, Steel et al. (2016) did not find benefits of reward on the retention of motor memory. Moreover, they found that the effects of punishment depended on the type of motor tasks. Punishment accelerated acquisition performance in a motor sequence task but inhibited acquisition performance in a force production task. These findings indicate that the intrinsic characteristics of motor tasks may determine the effects of incentive.

In brief, studies that examined visuomotor adaptation in normal healthy participants demonstrated that both sensory feedback and motivational feedback can drive visuomotor adaptation, but the two types of feedback have different effects and connect with different neural underpinnings. Morover, reward and punishment may

also have different effects on visuomotor adaptation and consolidation of visuomotor adaptation memory in young healthy participants, with punishment accelerating visuomotor adaptation but reward enhancing retention/consolidation of visuomotor adaptation memory.

This set of studies aimed to further uncover the effects of reward and punishment on visuomotor adaptation and consolidation of visuomotor adaptation memory in young healthy adults. By manipulating delivery probability of reward and punishment, the distinct effects of reward and punishment on visuomotor adaptation and consolidation of visuomotor adaptation memory were further demonstrated. By controlling sensory feedback of the reaching cursor to control the involvement of explicit learning and implicit learning in visuomotor adaptation, it was uncovered that the competition between explicit learning and implicit learning likely contributed to the distinct effects of reward and punishment on visuomotor adaptation and consolidation of visuomotor adaptation memory.

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CHAPTER 2. LITERATURE REVIEW

Effects of reward and punishment on motor adaptation/learning

How reward and punishment influence human motor learning has not been extensively studied until recent years. Several lines of research from implicit motor sequencing (serial reaction time task) (Wächter, et al., 2009), manual tracking (Abe, et al., 2011), and motor adaptation (Galea, et al., 2015) showed potentially distinct effects of reward and punishment on acquisition of motor memory and consolidation of motor memory. In this section, literature on the effects of reward and punishment is reviewed. Possible factors that may impact the influences of reward and punishment are discussed.

Wächter, Lungu, Liu, Willingham, and Ashe (2009) found in an implicit motor sequence learning study that rewards accelerated the learning but punishment only improved motor performance of healthy human participants. Abe and colleagues (2011) showed in a motor tracking study that rewarded participants retained much performance for longer time even at 30 days after training but punished participants and controls showed significant forgetting only after 6-hour-delay, despite comparable performance immediately after training in the three groups.

Nikooyan and Ahmed (2015) reported the latest evidence that reward feedback can also drive motor adaptation when an abrupt visual perturbation occurs. They designed a visuomotor adaptation task in which participants made reaching-out-and-back movements, during which the motion of the cursor underwent an abrupt 30°

counterclockwise rotation with respect to the motion of the reaching arm. After familiarization trials in which all participants received visual feedback of the cursor position, one group practiced with cursor position feedback and the other group had no visual feedback in practice. Both groups received reward to learn to adapt to the abrupt visual perturbation. The reward was provided as a trial score that ranged from 0 to 1,000 and depended on a linear or cubic function connected with endpoint error, which makes the reward feedback more informative. Their results demonstrated that reward feedback alone can drive the adaptation to the abrupt cursor rotation, but the combination of reward and sensory feedback accelerated the visuomotor adaptation.

In a more recent motor adaptation study, Kooij and Overvliet (2016) applied binary (success or fail) reward to young healthy participants when they learned a three dimensional pointing adaptation task. They found that the binary reward feedback together with endpoint spatial error feedback lead to successful adaptation, but different from Nikooyan and Ahmed (2015), the binary reward feedback alone did not induce adaptation. Together, these results indicate that the additional information gained from a scoring system may be an important component in motivational feedback.

Different from prior studies that used virtual reward feedback such as target explosion or score, Galea, Mallia, Rothwell, and Diedrichsen (2015) further demonstrated that monetary reward and punishment had dissociable effects on visuomotor adaptation. They provided participants with monetary reward or

punishment based on endpoint errors in the adaptation phase in two reaching tasks. In a rather difficult adaptation task, the hand cursor was alternatively rotated 15° clockwise (CW) or counterclockwise (CCW) in a random way. In a relatively easier adaptation task, the hand cursor was rotated 30° CCW. The researchers found different effects of punishment and reward on adaptation and retention. Specifically, punishment caused significantly the fastest adaptation in both the 15° alternating cursor rotation and the 30° CCW fixed cursor rotation. In contrast, reward showed no enhancement in adaptation compared to the control group without motivational feedback received. However, reward caused greater retention that was measured by adaptation performance in the blocks without visual cursor position feedback and participants executed reaching only based on the memory of previous practice. The findings indicate that punishment and reward may affect acquisition and consolidation of motor adaptation memory differently.

However, different from above reviewed studies, Steel et al. (2016) did not find benefits of reward on the retention of motor memory. Moreover, they found that the effects of punishment depended on the type of motor tasks. They trained participants in either a serial reaction time task or a force production task. Reward showed no offline consolidation benefits in neither the serial reaction time task nor the force production task. Punishment contributed to the faster decrease of reaction time in the serial reaction time but impaired performance in the force production task.

In short, recent findings revealed potential dissociable effects of reward and punishment on motor adaptation/learning and the consolidation of motor memory. Several factors may constrain the effects of reward and punishment, including the type of motor tasks, the intrinsic natures of reward or punishment distribution such as probability and magnitude, the underlying processes in motor adaptation/learning, and neural underpinnings related to motor learning and reward processing.

Influence of intrinsic features of reward and punishment

A choice or action is explicitly or implicitly associated with an outcome that has subjective value to the mover. The assumption of maximizing the potential value of a choice plays a prominent role in economic and current decision-making theories. The type, quantity, probability, and time delay are critical dimensions that affect the subjective value of an outcome associated with a choice or decision (Shizgal, 1997). It is proposed that prediction errors that represent the difference between predicted and realized subjective value can optimize decision making and cause learning (Lak, Stauffer, & Schultz, 2014; Hollerman & Schultz, 1998), and both the magnitude and probability of reward influence the coding of prediction errors (Fiorillo, Tobler, & Schultz, 2003). Meanwhile, some neural imaging studies reported potential neural correlates of representing the quantity and probability of reward such as ventral striatum and media prefrontal cortex (Knutson, Taylor, Kaufman, Peterson, & Glover, 2005; Kable & Glimcher, 2007).

The probability of reward was originally manipulated in animal conditioning studies that reported benefits of randomly or quasi-randomly distributed reward. Three probabilities of reward distribution, 100%, 50%, and 0%, were frequently applied in conditioning and instrumental learning studies. From the perspective of uncertainty, probability of 50% introduces maximal uncertainty, while probabilities of 100% and 0% induces minimal uncertainty.

The performance of animals that were provided with random or quasi-random reward could become equal to or exceed that of animals that were provided with consistent reward in every trial (for review, Bitterman & Schoel, 1970). Fiorillo, Tobler, and Schultz (2003) found in a monkey-conditioning task that monkey's licking duration increased with the probability of liquid reward. Animal studies on Pavlovian conditioning and instrumental learning revealed that 100% rewards lead to faster acquisition, but 50% rewards induced slower extinction (Jenkins and Stanley 1950; Padilla 1967; Haselgrove et al. 2004; Prados et al. 2008). In a human conditioning study (Au Yeung et al. 2014), young adults were randomly allocated to complete reinforcement (100%) conditioning, partial reinforcement (here 62.5%) conditioning, or control (0%). Complete reinforcement produced larger initial placebo analgesia (pain relief) in the conditioning phase, but the placebo analgesia also extinguished much faster in the test phase without reinforcement provided, compared to that analgesia generated by partial reinforcement.

In a movement sequence study, Dayan et al. (2014) trained human participants to learn a movement sequence that had to be completed within eight seconds in a trial. In the training phase, participants were provided with monetary rewards with the probability of 100%, 50%, 75% and 25% (these latter two were collapsed because of no performance difference). They found that, compared to other groups, the group with 50% reward learned much faster in the training phase and retained more skillful performance in the one-week post-training test. These findings, together with the conditioning work (Au Yeung et al. 2014), reflect that probability of reward differently influenced the acquisition of a skill from retention of a skill, specifically that 50% probability resulted in better retention. As to the influence of probability of punishment, we know very little.

Underlying processes of motor adaptation

It is still unclear why reward and punishment have different effects on motor adaptation/learning and motor memory. One possibility is that reward and punishment may interact with different underlying learning processes. Motor adaptation has been demonstrated to involve multiple underlying processes.

Multiple underlying processes have been proposed to co-exist during motor adaptation. Traditionally, it was thought to be an implicit process, but findings indicate that motor adaptation can be influenced by the interplay between explicit process and implicit process. Implicit process may be modulated by sensory prediction error and expressed as slow and monotonic change in performance; explicit

process may be modulated by end-point error or explicit strategy and instruction, and achieved by initially large then smaller explorations of movement direction biased toward the correct solution (Taylor, Krakauer, & Ivry, 2014).

Smith, Ghazizadeh, and Shadmehr (2006) proposed fast and slow processes contributing to motor adaptation. Specifically, fast process responds strongly to error and adapts quickly but shows poor retention, whereas slow process responds weakly to error and adapts gradually but shows good retention. The fast and slow processes together enable the motor system to compensate for environmental perturbations. This proposal is consistent with an earlier proposal on fast learning and slow learning underlying skill learning (Karni, et al., 1998) and corresponding evidence from neural plasticity (Costa, Cohen, & Nicolelis, 2004). Fast learning is an initial improvement phase, induced by limited training; slow learning consists of delayed, incremental gains in performance triggered by continued practice.

Huang, Haith, Mazzoni, and Krakauer (2011) proposed model-based learning and model free learning based on their findings on savings in motor adaptation. Specifically, model-based learning is guided by an internal forward model of the environment updated by sensory prediction errors, whereas model-free learning is driven by reinforcement of task success. They thought that model-based learning and model-free learning may be cooperative in motor adaptation, with model-based learning guiding initial adaptation to a suitable level and then model-free learning becoming more prominent in the form of use-dependent plasticity.

These proposed underlying processes of motor adaptation may have interconnection. For instance, fast learning may be model-based and slow learning may be model-free (Huang, et al., 2011), and fast learning may be explicit (Keisler & Shadmehr, 2010). McDougle et al. (2015) further demonstrated through computational simulation that the fast process and the slow process proposed by Smith et al. (2006) can be respectively captured by explicit learning and implicit learning.

Explicit learning and implicit learning not only interact to influence online motor adaptation but also offline motor memory consolidation. Poldrack and Packard (2003) reviewed findings from animal studies and concluded that multiple memory systems were activated simultaneously in various learning tasks and interaction between some memory systems, such as medial temporal lobe and basal ganglia memory systems, were competitive in nature. Brown and Robertson (2007) demonstrated how explicit memory influenced the offline consolidation of motor sequence memory in a serial reaction time task (SRTT) study. SRTT was thought to be an implicit motor learning task, but participants may show an ability to verbally describe items within the movement sequence. In this study, two groups of participants learned a word list or counted number of vowels within nonsense letter strings immediately after the SRTT training and performance test. The immediate motor performance of the two groups showed no statistical difference in performing the SRTT task. However, in the 12-hour-late retention test, the word-list-learning group showed clear offline improvement in performing the SRTT sequence, but the

vowel-counting group showed no offline improvement. The researchers thought that the offline gain in the word-list learning group was due to the word-list learning task interfering or suppressing the explicit component of motor sequence memory. They proposed that the offline motor memory consolidation relies on the disengagement of competition between explicit and implicit memory systems.

Keisler and Shadmehr (2010) further demonstrated how offline consolidation of motor adaptation memory was affected by competition between explicit and implicit memory systems in a series of force field motor adaptation experiments by controlling training amount. They found that a word-pair learning task did not change the offline consolidation of motor adaptation memory formed after extended training (implicit memory) but the word-pair learning task altered the offline consolidation of motor adaptation memory formed after short training (explicit and implicit memory systems). In one experiment, immediately after 384 trials of adaptation to a force field, one group studied pairs of English words for three minutes and the other group did nothing but rested for three minutes. The two groups showed comparable immediate retention performance tested with error-clamp trials, in which the force field was still applied but no performance error was perceived by participants. In another experiment in which the retention test was delayed to six hours after the extended adaptation training (384 trials), the word-pair learning group also had similar retention performance as the control group. These showed that the offline consolidation of motor adaptation memory formed after extended training was not altered by the word-pair learning task. Differently, in one experiment, in the three

minutes immediately after 20 trials of adaptation to a force field, one group studied pairs of English words, another group counted number of vowels in letter strings, and the third group did nothing but rest. Compared to the other two groups, the word-pair learning group showed worse retention performance tested with error-clamp trials. In another experiment, the retention test was delayed to six hours after short adaptation training (20 trials), and the word-pair learning group showed better retention performance compared to other two groups, thus showing offline consolidation of motor adaptation memory formed after short training was altered by the word-pair learning task. The researchers conjectured that motor adaptation memory formed after extended training was mostly implicit and so the word-pair learning task did not affect its offline consolidation. In contrast, motor adaptation memory formed after short training involved explicit and implicit memory components so the word-pair learning task suppressed the offline consolidation of explicit component and improved the offline consolidation of implicit component of motor memory.

All these findings support the interactive influence of explicit and implicit learning during motor skill acquisition (Smith et al. 2006; Taylor et al. 2014; McDougle et al. 2015) and the offline consolidation of motor memory (Brown et al. 2007; Keisler et al. 2010). Explicit and implicit learning may function in synergy to drive online acquisition of motor skill, but the explicit memory component may compete with the implicit memory component to influence offline consolidation and expression of motor memory.

Neural underpinnings in motor adaptation and reward processing

Brain areas mainly reported to be involved in motor adaptation include the cerebellum (Tseng, et al., 2007), primary motor cortex (M1) (Wise, Moody, Blomstrom, & Mitz, 1998), and posterior parietal cortex (PPC) (Tanaka, Sejnowski, & Krakauer, 2009). In the past decade, the cerebellum was demonstrated to be involved in predicting the sensory consequences of action (Blakemore, Frith, & Wolpert, 2001; Miall R. C., Christensen, Cain, & Stanley, 2007) and encoding of sensory prediction errors (Schlerf, Ivry, & Diedrichsen, 2012). It is also thought to be involved in driving the acquisition of motor adaptation based on sensory prediction error (Tseng, et al., 2007) or providing sensory prediction error to PPC and M1, which were also thought to be the likely sites for the occurrence of visual motor remapping (Tanaka, et al., 2009).

There is substantial evidence that dopamine and the striatum are involved in reward and punishment processing, with the striatum showing different hemodynamic responses to monetary outcomes of different reward and punishment valence in humans and animals (Delgado, 2007). Pessiglione and collaborators (2007) measured brain activity in an fMRI imaging study by varying the amount and reportability of monetary rewards before participants exerted hand-grip force, which was used as a behavioral measurement of financial motivational effect. They demonstrated that both conscious or unconscious motivational effects were underpinned by engagement of a specific basal forebrain region consisting of the ventral striatum, ventral pallidum, extended amygdala, and basal nucleus of Meynert. The ventral striatum has been

reported to be involved in reward processing during learning and is also the main input to the ventral pallidum, which the researchers thought may mediate motivational processes and modulate supplementary motor are (SMA) activity, which in turn drives muscular contractions via primary motor area (M1).

As to the potentially dissociable effects of reward and punishment demonstrated in healthy participants' motor adaptation (Galea, et al., 2015), the two modes of motivational feedback may act on different neural systems and be mediated by different neural transmitters. Reward may be mediated through the dorsal striatum and punishment through the insula (Wächter, et al., 2009). Dopamine was involved in learning from reward feedback but it was not necessary for learning from punishment feedback, which could be mediated by serotonin (Delgado, 2007). Galea and co-workers (2015) proposed that punishment-induced improvements in adaptation and re-adaptation phase in healthy participants may be due to the increased cerebellar sensitivity to sensory prediction errors associated with punishment stimuli, while reward-induced benefits in retention of motor learning may be a consequence of a stronger memory trace for the new visuomotor transformation formed in the cerebral cortex, especially the primary motor cortex (M1), which has direct projections from neurons releasing dopamine. However, there is no direct evidence supporting the influence of reward and punishment on M1 and the cerebellum.

The primary motor cortex is thought to be involved in the retention of motor memory (Richardson, et al., 2006) but not in the acquisition of motor adaptation

(Galea, Vazquez, Pasricha, Orban De Xivry, & Celnik, 2011). However, the finding that repetitive transcranial magnetic stimulation (rTMS) over M1 did not disrupt the retention of dynamic force field adaptation indicates the learning of dynamic adaptation may be stored in a more distributed manner and possibly outside M1 (Baraduc, Lang, Rothwell, & Wolpert, 2004). Moreover, it was demonstrated that reward can induce changes of excitability of M1 (Kapogiannis, Campion, Grafman, & Wassermann, 2008; Thabit, et al., 2011).

The cerebellum and basal ganglia were traditionally thought to be unconnected subcortical structures, but they were recently demonstrated to have reciprocal disynaptic connection (from subthalamic nucleus to the cerebellum and from dentate nucleus to the striatum), possibly to support two-way communication between them and form an integrated functional network (Bostan, Dum, Strick, & Graybiel, 2010). This is also reflected by the evidence of abnormal activation of the cerebellum in some patients with Parkinson's disease (for review, Wu & Hallett, 2013). In contrast to the traditionally held motor function, the cerebellum was also reported to be associated with motivation and emotion (Schutter & Honk, 2005; Strick, Dum, & Fiez, 2009), associative learning (Bellebaum & Daum, 2011), and reward-based reversal learning (Thoma, Bellebaum, Koch, Schwarz, & Daum, 2008). There are studies indicating that the cerebellar activation was associated with fear conditioning and negative affective states, as well as related to positive mood (for review, Schutter & Honk, 2005).

In brief, the findings supporting the roles of M1 and the cerebellum in visuomotor adaptation are inconsistent, and there is also no direct evidence indicating how reward and punishment affect their functioning in motor adaptation. Moreover, the likely integrated functional network of the cerebellum and basal ganglia challenges the dichotomy of their roles in learning, that of the cerebellum implementing error-based learning and the basal ganglia reinforcement learning.

In summary, published studies revealed distinct effects of reward and punishment on acquisition and consolidation of motor memories in a series of motor tasks. Several factors may modulate the impact of reward and punishment but direct test of possible modulation and cause is lacking. Probability of reward and punishment distribution is a critical intrinsic factor determining the subjective perception of incentive. The first experiment in this research tested the modulation of probability on the effects of reward and punishment in visuomotor adaptation. Explicit process and implicit process are two main underlying processes in motor adaptation. The second and the third experiments in this research explored the role explicit process played in the dissociable effects of reward and punishment.

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CHAPTER 3. PROBABILITY DIFFERENTLY MODULATING THE EFFECTS OF REWARD AND PUNISHMENT ON VISUOMOTOR ADAPTATION

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Abstract

Recent human motor learning studies revealed that punishment seemingly accelerated motor learning but reward enhanced consolidation of motor memory. It is not evident how intrinsic properties of reward and punishment modulate the potentially dissociable effects of reward and punishment on motor learning and motor memory. It is also not clear what causes the dissociation of the effects of reward and punishment. By manipulating probability of distribution, a critical property of reward and punishment, the present study demonstrated that probability had distinct modulation on the effects of reward and punishment in adapting to a sudden visual rotation and consolidation of the adaptation memory. Specifically, two probabilities of monetary reward and punishment distribution, 50% and 100%, were applied during young adult participants adapting to a sudden visual rotation. Punishment and reward showed distinct effects on motor adaptation and motor memory. The group that received punishments in 100% of the adaptation trials adapted significantly faster than the other three groups, but the group that received rewards in 100% of the adaptation trials showed marked savings in

re-adapting to the same rotation. In addition, the group that received punishments in 50% of the adaptation trials that were randomly selected also had savings in re-adapting to the same rotation. Sensitivity to sensory prediction error or difference in explicit process induced by reward and punishment may likely contribute to the distinct effects of reward and punishment.

Keywords: reward, punishment, visuomotor adaptation, sensorimotor learning, savings

Introduction

The effects of reward and punishment on animal and human behavior have long been investigated in many domains like animal learning (Thorndike 1933), human cognition (Carnagey and Anderson 2005), and human social behavior (Balliet et al. 2011). In contrast, how reward and punishment influence human motor learning has not been extensively studied until recent years. Several lines of research from implicit motor sequencing (serial reaction time task) (Wächter, et al., 2009), manual tracking (Abe, et al., 2011), and motor adaptation (Galea, et al., 2015) showed potentially distinct effects of reward and punishment on acquisition of motor skills and consolidation of motor memory. Moreover, the impact of reward and punishment on skill learning likely depends on task demands (Steel et al. 2016). In this study, we

investigated the effects of reward and punishment on visuomotor adaptation and how probability of incentive distribution influenced the effects of reward and punishment.

Motor adaptation, a specific form of motor learning, was once thought to be driven by sensory prediction error (Tseng et al. 2007), which is the difference between the expected movement outcome and the actual movement outcome. However, motor adaptation was later found to be also driven by reward feedback (Izawa and Shadmehr 2011; Nikooyan and Ahmed 2015).

Nikooyan and Ahmed (2015) used a visuomotor adaptation task to explore the effects of sensory feedback and motivational feedback on motor learning. Young healthy participants were rewarded by using a linear or a cubic scoring system when they learned to adapt to an abrupt 30° counterclockwise (CCW) visual rotation of a cursor in doing fast reaching movements. They demonstrated that reward feedback alone drove adaptation to the abrupt visual rotation, and the combination of reward and sensory feedback accelerated the visuomotor adaptation.

In a more recent motor adaptation study, van der Kooij and Overvliet (2016) applied binary (success or fail) reward to young healthy participants when they learned a three dimensional pointing adaptation task. They found that the binary reward feedback together with endpoint spatial error feedback lead to successful adaptation, but different from Nikooyan and Ahmed (2015), the binary reward feedback alone did not induce adaptation. Together, these results indicate that the

additional information gained from a scoring system may be an important component in motivational feedback.

In another visuomotor adaptation study, Galea and colleagues (2015) further demonstrated that monetary punishment and reward had dissociable effects on visuomotor adaptation and retention of the adaptation memory. Specifically, the researchers provided young healthy adults with monetary reward or punishment according to endpoint performance error while learning to adapt to an abrupt 30° CCW cursor rotation, and they found that the punishment group had faster adaptation when visual feedback of the cursor was provided but the reward group had better retention of the acquired adaptation when visual feedback of the cursor was not provided.

Findings in these studies manifest distinct effects of reward and punishment on motor adaptation and retention of the adaptation memory. A common feature of these studies is the manipulation of the type of incentive. However, it is not clear how parameters of reward and punishment, such as probability of distribution, affect the impact of reward and punishment on motor adaptation and consolidation of the adaptation memory. Perception of the subjective value associated with reward is affected by its probability, magnitude, and timing of distribution (Tobler et al. 2005; Shizgal 1997). Three probabilities of reward distribution, 100%, 50%, and 0%, were frequently applied in conditioning and instrumental learning studies. From the

perspective of uncertainty, probability of 50% introduces maximal uncertainty, while probabilities of 100% and 0% induces minimal uncertainty.

Animal studies on Pavlovian conditioning and instrumental learning revealed that 100% rewards lead to faster acquisition but 50% rewards induced slower extinction (Jenkins and Stanley 1950; Padilla 1967; Haselgrove et al. 2004; Prados et al. 2008). In a human conditioning study (Au Yeung et al. 2014), young adults were randomly allocated to complete reinforcement (100%) conditioning, partial reinforcement (here 62.5%) conditioning, or control (0%). Complete reinforcement produced larger initial placebo analgesia (pain relief) in the conditioning phase, but the placebo analgesia also extinguished much faster in the test phase without reinforcement provided, compared to that analgesia generated by partial reinforcement.

In a movement sequence study, Dayan et al. (2014) trained human participants to learn a movement sequence that had to be completed within eight seconds in a trial. In the training phase, participants were provided with monetary rewards with the probability of 100%, 50%, 75% and 25% (these two were collapsed because of no performance difference). They found that, compared to other groups, the group with 50% reward learned much faster in the training phase and retained more skillful performance in the one-week post-training test. These findings, together with the conditioning work (Au Yeung et al. 2014), reflect that probability of reward may differently influence the acquisition of a skill from retention of a skill, specifically

that 50% probability results in better retention. As to the influence of probability of punishment, we know very little.

In the extant literature, there is no motor adaptation study in which the probability of reward or punishment is examined. The investigation of how the probability of reward and punishment affects motor adaptation can further our understanding of the impact of reward and punishment on human motor adaptation. Practically, findings in this line of research are also helpful to optimize the distribution of reward or punishment in real contexts such as movement skill training and rehabilitation training.

In the present study, a visuomotor adaptation task was employed to investigate the impact of probability of reward and punishment on human participants' learning and consolidation of the visuomotor adaptation. Two probabilities, 100% and 50%, of reward and punishment distribution were administered during the adaptation phase. Reward and punishment were provided in the gradient form of winning or losing money based on end-point accuracy. Different from previous studies, the present study applied a 50° clockwise rotation. Morehead and colleagues (2015) found that the size of rotation affected savings in visuomotor adaptation. Savings means faster relearning of the same task the second time compared to the initial learning (Shadmehr et al. 2010). The mechanism underlying savings in motor learning is still not clear.

In the present study, the acquisition of the rotation change was measured during the adaptation phase, and the consolidation of visuomotor adaptation memory was measured by savings and performance change in the phase in which continuous visual feedback was withdrawn. It was hypothesized that punishment would result in faster visuomotor adaptation, while reward would result in better consolidation of the adaptation memory. It was also hypothesized that 50% of reward and punishment distribution would be more effective, respectively, than 100% of reward and punishment distribution in consolidation of the adaptation memory.

Method

Participants

Forty-four undergraduate students participated in this study. The mean age of participants was 20 years (range 18-22, SD 1.3, 13 males). All participants reported having normal health conditions and being right-handed. The handedness was also checked with Edinburgh Handedness Inventory (Oldfield, 1971). The study was approved by the University Institute Review Board (see appendix for IRB approval). Before participation, all participants provided their informed consent.

Apparatus

A desktop computer (Dell), a digitize tablet and pen (Wacom), and a customized Matlab (Mathworks) software were used in the data collection. The computer monitor was 37.5 cm wide, 30.5 cm high and had a resolution of 1024 by 768 pixels. The monitor was placed vertically and 50 cm away from participants'

foreheads. Participants were seated in an arm chair with the chair height adjusted such that their eyes were level with the center of the monitor. The monitor displayed a white-edge start square (5 mm by 5 mm), a white circular cursor (3 mm diameter), and a circular target (6 mm diameter) in a black full-screen window. The start square was fixed at the center of the monitor and was displayed throughout the experiment. The target was displayed vertically above (90° direction) and 10 cm away from the start square. The movement of the cursor was controlled by participants with the Intuos digitize pen. Participants' direct vision of their hands was blocked by a level surface.

Task

When participants moved the cursor into the center of the start square, the target appeared red and 1200 ms later, the target changed to green. The appearance of the green target was the signal for participants to move the cursor to shoot the target. To control the influence of error correction, participants were instructed to shoot the cursor through the target in a non-curving path and not to correct the moving trajectory of the cursor. After the center of the cursor moved out an invisible circular boundary where the center of the target was located (see Fig. 1), both the cursor and the target disappeared, and an auditory feedback of "too fast" or "too slow" was played if the movement time of the cursor was less than 100ms or more than 600ms. Before moving the cursor back to the start square, participants were instructed to pause to make the moving-out and moving-in of the cursor discontinuous.

Experimental Design

Participants were randomly assigned into four groups, 11 in each group. Participants in each group were provided with differential monetary incentives in the adaptation phase. The 100%-reward group won money in every adaptation trial. The 50%-reward group won money in 50% of adaptation trials that were randomly selected. The 100%-punishment group lost money in every adaptation trial. The 50%-punishment group lost money in 50% of adaptation trials that were randomly selected. The random selection of 50% of adaptation trials that were rewarded or punished did not have any extreme series such as massed eight continuous reward, punishment, or null incentive trials during any period of the adaptation phase.

Procedures

The structure of the test was similar to that in Galea and colleagues (2015). Fig. 1 illustrates the conditions in the test. The test consisted of 80 baseline trials, 200 adaptation trials with continuous visual feedback of the cursor, 200 no-vision adaptation trials without visual feedback of the cursor, 100 washout trials, and 100 re-adaptation trials with continuous visual feedback of the cursor. In the baseline phase and washout phase, movement of the cursor was congruent with the moving of the pen. In the adaptation, no-vision, and re-adaptation phases, the movement of the cursor was rotated by 50° clockwise (CW) relative to the moving of the pen. In the baseline, adaptation, washout, and re-adaptation phases, the visual feedback of the cursor trajectory was provided when the cursor was in the invisible circular boundary

and was withdrawn when the cursor moved beyond the invisible circular boundary. In the no-vision phase, the cursor was only displayed when it was in the start square, participants were informed that moving dynamics of the cursor was the same as that in the adaptation phase and they were also instructed to make non-curving shooting movements. The rest interval between phases was one minute.

In the beginning of the adaptation phase, the two punishment groups were provided with 14 dollars, and then they lost money from 0 to 7 cents in an adaptation trial with the probability of 100% or 50%. The two reward groups won money from 0 to 7 cents in an adaptation trial with the probability of 100% or 50%. How much money a participant won or lost from an adaptation trial was determined by the endpoint error (the angular distance from the cursor to the target when the cursor moved through the invisible circular boundary) according to the following rule:

Reward. 7 cents: <2° endpoint error; 6 cents: <9° endpoint error; 5 cents: <16 ° endpoint error; 4 cents: <23° endpoint error; 3 cents: <30° endpoint error; 2 cents: <37° endpoint error; 1 cent: <44° endpoint error; 0 cent: ≥44° endpoint error.

Punishment. 0 cent: <2° endpoint error; -1 cent: <9° endpoint error; -2 cents: <16 ° endpoint error; -3 cents: <23° endpoint error; -4 cents: <30° endpoint error; -5 cents: <37° endpoint error; -6 cents: <44° endpoint error; -7 cents: ≥44° endpoint error.

Participants were not informed of this incentive rule. They were instructed that the amount of money one could win or lose in an adaptation trial was determined by accuracy of the cursor hitting the target, and they were encouraged to try their best to

maximize the money they could win or minimize the money they could lose. To balance the average amount of money the two reward groups could win, participants in the 50%-reward group were randomly selected to have five dollars to begin the adaptation phase or have five dollars added in the end of the adaptation phase. Specifically, participants that were randomly selected to have five extra dollars at the beginning of adaptation were informed of this at the beginning of adaptation, and participants that were randomly selected to gain five extra dollars at the end of adaptation were not informed of this at the beginning of adaptation but were informed of this at the end of adaptation. Participants in the 100%-reward group began in the adaptation phase with no money provided. Since we predicted that the 100%-punishment group would adapt much faster compared to the 50%-punishment group, participants in the two punishment groups were not provided with any extra money. When the cursor moved outside the invisible circular boundary, the cursor and the target disappeared and the amount of money a participant won or lost from that adaptation trial was displayed at the target position in red color in 48 font size. An "==" symbol was displayed to the 50%-reward and 50%-punishment groups after an adaptation trial in which they did not win or lose money. After the cursor re-entered the invisible circular boundary, the monetary feedback disappeared.

Data Analysis

Heading angle was the primary dependent variable used to assess adaptation performance and the consolidation of adaptation memory. The heading angle was

defined as the aiming angle created by the hand-held cursor when the cursor was midway (3cm) along the trajectory so to limit the role of corrective movements in measure of adaptation (McDougle et al. 2015). Cartesian X and Y coordinates of the cursor were recorded in 100 Hz frequency and further used to compute the heading angle and the endpoint error. The first trial of each phase was excluded in the analysis (Galea et al. 2015). Performance of each phase was based on the mean heading angle of pre-selected trials (Leow et al. 2012; McDougle et al. 2015). Specifically, mean heading angles of the last 15 baseline trials, the first 15 adaptation trials, the last 15 adaptation trials, the last 15 no-vision trials, the first 15 washout trials, the last 15 washout trials, and the first 15 re-adaptation trials were calculated.

One-state State Space Model (SSM) was also used to fit the heading angles across all adaptation trials and across all re-adaptation trials so to measure the overall adaptation rate and re-adaptation rate of each participant. The one-state SSM is represented by:

$$e_t = x_t + p_t$$

$$x_{t+1} = ax_t + be_t$$

Where e is the error experienced at trial t involving perturbation p, a is the retention rate of the previous state, and b is the learning rate (McDougle et al. 2015). The model was fit by applying the Matlab function fmincon to minimize the residual mean square (rms) error between the model simulation and the experimental data subject to the constraints $0<a<1$ and $-1<b<1$. Table 1 shows group mean fit parameter values of SSM.

SSM was also applied to fit data in the no-vision phase. The fitting results were poor when the learning parameter *b* was fixed to zero (for no error information was provided) as in Galea et al. (2015). Hence the fitting parameters for the no-vision data were not further analyzed.

Trial-by-trial change of heading angle was quantified to evaluate how reward and punishment feedback influenced adaptation. The degree change of heading angle on trial *t+1* after receiving a certain reward or punishment feedback on trial *t* was defined as the difference between the heading angle on trial *t+1* and the heading angle on trial *t* (Chen et al. 2017). To assess how the magnitude of reward or punishment feedback influenced the effects of reward or punishment on adaptation, reward feedback was categorized into small gain and big gain, and punishment feedback was categorized into big loss and small loss. Specifically, small gain was operationalized as reward feedback 0¢, +1¢, +2¢, and +3¢; big gain was operationalized as reward feedback +4¢, +5¢, +6¢, and +7¢; big loss was operationalized as punishment feedback -7¢, -6¢, -5¢, and -4¢; and small loss was operationalized as punishment feedback -3¢, -2¢, -1¢, and 0¢.

Savings was applied to assess offline consolidation of visuomotor adaptation memory. It was quantified by rate parameter *b* in exponential fitting of performance errors of the first 60 adaptation trials and fitting of performance errors of the first 60 re-adaptation trials (Morehead et al. 2015; Zarahn et al. 2008). Significant difference between parameter *b* in fitting adaptation data and re-adaptation data indicates savings occurred in re-adapting to the same rotation. The exponential fitting function used is:

$$e_n = \mathrm{a}e^{bn} + c$$

where e_n is the error experienced at trial n, which is the difference between heading angle and the perturbation applied. The nonlinear least square method provided by Matlab was applied in the exponential fitting. The range for *b* was constrained from -1 to 1.

Reaction time and movement time were secondary dependent variables. Reaction time (RT) was defined as the time from the target changed into green to the start of the cursor movement. Movement time (MT) was defined as the time from the start of the cursor moving to the time of the cursor moved out the invisible circular boundary. Reaction time was associated with movement preparation, which was found to play a role in the expression of motor learning and savings (Haith et al. 2015). To control the potential impact of motor preparation, trials with RT longer than one second and shorter than 80ms were excluded from analysis. The trials excluded in analysis accounted for 13% of total trials on average and there were no group differences in the number of excluded trials. The excluded trials did not bias the results according to comparison of analysis of all trials and analysis of trials with exclusion.

A 2×2 between-subjects ANOVA was administered to examine the effects of incentive (reward vs punishment) and probability (100% vs 50%) on adaptation, re-adaptation, and savings. Simple effect analysis was applied to assess significant interaction effects. When interaction was significant, main effects were not analyzed. A one-tailed paired-sample t test was used to test the occurrence of savings. A mixed

effects ANOVA with incentive and probability as between-subjects factors and phase as within-subject factor was used to test the group differences of RT and MT. Tukey honest significant difference (HSD) test was used in multiple post-hoc comparisons. Significance level was set at $p< 0.05$ in statistical tests. All data are reported as mean ± standard error (s.e.) across participants.

Results

Overview

Table 2 shows the mean heading angles and standard errors in the pre-selected trials in each phase. Illustrated by Fig. 2, which provides an overview of the mean heading angle throughout the testing phases, the four groups showed indiscriminate heading angles at the end of baseline. In the initial adaptation phase, the 100%-Punishment group increased the heading angle markedly faster than other groups, indicating faster adaptation in this group. In the final adaptation phase, the changing of heading angle slackened and group difference in heading angle were reduced. In the no-vision phase, all groups showed decreases in heading angles compared to the end of adaptation, but no group exhibited decay trends in heading angle. In the washout phase, all groups quickly drifted back to the baseline level and the mean heading angles of the last 15 washout trials were comparable. In the re-adaptation phase, all groups rapidly increased heading angles and group differences were not so pronounced. At the end of the experiment, the average amount of compensation, which was determined by the amount of money one won or lost in the adaptation phase, the four experimental groups

received was: the 50%-Reward group: $9.0±1.9 (won $4.0±1.9 and added $5), the 100%-Reward group: $9.3±2.5, the 50%-Punishment group: $10.5±1.9 (lost $3.5±1.9 and deducted from $14), and the 100%-Punishment group: $10.2±0.7 (lost $3.8±0.7 and deducted from $14).

Adaptation Phase

In the adaptation phase, the cursor moving direction was rotated by 50° CW. The optimal solution to counteract this rotation was to adjust the heading angle by 50° CCW, relative to the start square and the target direction. The change of the heading angle from baseline, especially in the first 15 trials, indicates the rate of adaptation. Fig. 3a shows the mean heading angles of the first 15 adaptation trials of the four experimental groups. A 2×2 between-subjects ANOVA was administered to examine the heading angle difference in the four experimental groups. The ANOVA revealed a significant interaction between incentive and probability on heading angle ($F(1,40)= 7.56$, $p= 0.009$, $\eta_p^2 = 0.16$). There was also a main effect of incentive ($F(1,40)= 4.12$, $p= 0.05$, $\eta_p^2 = 0.09$) but no main effect of probability ($F(1,40)= 2.53$, $p= 0.12$, $\eta_p^2 = 0.06$). Simple effect analysis on the significant interaction showed that 100%-Punishment group adapted faster than 100%-Reward group (mean heading angle difference= 19.31°, $F(1,40)= 11.42$, $p= 0.002$, $\eta_p^2 = 0.16$), and 100%-Punishment group adapted faster than 50%-Punishment group (mean heading angle difference= 17.54°, $F(1,40)= 9.42$, $p= 0.004$, $\eta_p^2 = 0.18$).

One-state SSM was administered to fit the heading angles across all adaptation trials so to measure the overall adaptation rate. The SSM fitting was aimed to minimize the residual error between participants' data and the model simulation. Fig. 3b shows the parameter *b* in the SSM, which is thought to represent the adaptation rate (McDougle, et al., 2015). A 2×2 between-subjects ANOVA revealed a significant interaction of incentive and probability on the parameter *b* ($F(1,40)= 5.05$, $p= 0.03$, $\eta_p^2 = 0.11$). There were no main effect of incentive ($F(1,40)= 2.76$, $p= 0.10$, $\eta_p^2 = 0.06$) but the main effect of probability was approaching significance ($F(1,40)= 3.67$, $p= 0.06$, $\eta_p^2 = 0.08$). Simple effect analysis on the significant interaction showed that 100%-Punishment group adapted faster than 100%-Reward group (mean parameter *b* difference= 0.11, $F(1,40)= 7.64$, $p= 0.009$, $\eta_p^2 = 0.16$), and 100%-Punishment group adapted faster than 50%-Punishment group (mean parameter *b* difference = 0.12, $F(1,40)= 8.67$, $p= 0.005$, $\eta_p^2 = 0.18$). Parameter *a* of SSM is thought to indicate retention rate (McDougle, et al., 2015). A 2×2 between-subjects ANOVA showed no main effects of incentive ($F(1,40)= 1.49$, $p= 0.23$, $\eta_p^2 = 0.04$) and probability ($F(1,40)= 0.95$, $p= 0.34$, $\eta_p^2 = 0.02$) and no significant interaction ($F(1,40)= 1.36$, $p= 0.25$, $\eta_p^2 = 0.03$).

How reward and punishment feedback influenced adaptation was assessed by trial-by-trial change of heading angle. To minimize punishment or maximize reward, participants might make greater adjustment in next reaching after receiving a big loss (-7¢, -6¢, -5¢, -4¢) or a small gain (0¢, 1¢, 2¢, 3¢) than after receiving a small loss (-3¢, -2¢, -1¢, 0¢) or a big gain (4¢, 5¢, 6¢, 7¢). Fig. 4a shows trial-by-trial change of

heading angle after receiving small gain/big loss or big gain/small loss in the 100%-Reward group and the 100%-Punishment group. Fig. 4b shows trial-by-trial change of heading angle after receiving small gain/big loss or big gain/small loss or no incentive in the 50%-Reward group and the 50%-Punishment group. In all the four groups, participants showed evident trial-by-trial increase of heading angle after receiving small gain or big loss but negligible trial-by-trial change of heading angle after receiving big gain or small loss or no incentive. Moreover, participants had greater trial-by-trial increase of heading angle after receiving big loss than receiving small gain. In the 100%-Reward group and 100%-Punishment group, a 2×2 between-subjects ANOVA showed a main effect of magnitude of incentive ($F(1,40)= 20.16$, $p< 0.001$, $\eta_p^2 = 0.34$), a trend for incentive ($F(1,40)= 3.28$, $p= 0.078$, $\eta_p^2 = 0.076$), and significant interaction between magnitude of incentive and incentive ($F(1,40)= 5.14$, $p= 0.029$, $\eta_p^2 = 0.11$). Simple effect analysis on the significant interaction showed that the 100%-Punishment group had greater trial-by-trial change of heading angle after receiving big loss than after receiving small loss (mean difference= 7.07°, $F(1,40)= 22.82$, $p< 0.001$, $\eta_p^2 = 0.36$), the 100%-Punishment group also had greater trial-by-trial change of heading angle after receiving big loss than the 100%-Reward group after receiving small gain (mean difference=4.28°, $F(1,40)= 8.31$, $p= 0.006$, $\eta_p^2 = 0.17$). In the 50%-Reward group and 50%-Punishment group, a 2×3 between-subjects ANOVA showed a main effect of magnitude of incentive ($F(2,55)= 6.84$, $p= 0.002$, $\eta_p^2 = 0.20$), but no main effect for incentive ($F(1,55)= 1.14$, $p= 0.29$, $\eta_p^2 = 0.018$) and no significant interaction between magnitude of incentive and incentive ($F(2,55)= 2.11$, $p= 0.13$, $\eta_p^2 = 0.07$).

No-vision Phase

In the no-vision phase, the 50° CW rotation was still applied to the cursor and once the cursor was moved outside the start square, no visual feedback of the cursor was provided, thus participants had to rely on their memory of previous adaptation training to successfully hit the target. The change of heading angle from the adaptation phase reflects retention of the previous adaptation. This can be measured by the difference between the mean heading angle of last 15 no-vision trials and the mean heading angle of last 15 adaptation trials. All four groups showed decreases of the mean heading angles in the last 15 no-vision trials compared to the last 15 adaptation trials, indicating poor retention. Specifically, the 100%-Reward group had a decline of 12.3° (s.e.: 2.9°) in mean heading angle, the 50%-Reward group 6.8° (s.e.: 3.6°), the 100%-Punishment group 9.7° (s.e.: 2.4°), and the 50%-Punishment group 5.0° (s.e.: 4.1°). A 2×2 between-subjects ANOVA revealed no main effects of incentive ($F(1,40)= 0.43$, $p= 0.52$, $\eta_p^2 = 0.01$) or probability ($F(1,40)= 2.28$, $p= 0.14$, $\eta_p^2 = 0.05$) and no significant interaction ($F(1,40)= 0.014$, $p= 0.91$, $\eta_p^2 = 0.00$) on the mean heading angle difference, indicating that the four groups decayed previous adaptation in a comparable amount.

Washout Phase

In washout phase, no rotation was applied to the cursor. Hence participants should show after-effects of discontinuing the previously administered rotation, i.e. over-compensating in the opposite direction. With practice, participants should

gradually decrease heading angle back to 0° so to successfully hit the target. Based on 2×2 between-subjects ANOVA, the mean heading angle of first 15 washout trials showed no main effects of incentive ($F(1,40)= 0.74$, $p= 0.39$, $\eta_p^2 = 0.02$) and probability ($F(1,40)= 2.75$, $p= 0.10$, $\eta_p^2 = 0.06$), and no significant interaction ($F(1,40)= 0.02$, $p= 0.89$, $\eta_p^2 = 0.00$), indicating comparable after-effects among the four experimental groups. The mean heading angle of last 15 washout trials showed no main effects of incentive ($F(1,40)= 1.02$, $p= 0.32$, $\eta_p^2 = 0.02$) and probability ($F(1,40)= 1.69$, $p= 0.20$, $\eta_p^2 = 0.04$), and no significant interaction ($F(1,40)= 0.76$, $p= 0.39$, $\eta_p^2 = 0.02$), suggesting comparable washout of the adaptation training among the four groups.

Re-adaptation Phase

In the re-adaptation phase, the 50° CW rotation was again added to the cursor movement. Fig. 4a shows the mean heading angles of the first 15 re-adaptation trials in the four groups. A 2×2 between-subjects ANOVA showed no main effect of incentive ($F(1,40)= 0.47$, $p= 0.50$, $\eta_p^2 = 0.01$) and no significant interaction ($F(1,40)= 0.07$, $p= 0.79$, $\eta_p^2 = 0.00$), but the main effect of probability approached significance ($F(1,40)= 3.74$, $p= 0.06$, $\eta_p^2 = 0.08$). One-state SSM was also administered to fit the heading angles across all re-adaptation trials so to measure the overall re-adaptation rate. Fig. 4b shows the parameter *b* in the SSM. A 2×2 between-subjects ANOVA showed no main effect of incentive ($F(1,40)= 2.26$, $p= 0.14$, $\eta_p^2 = 0.05$) and no significant interaction ($F(1,40)= 0.047$, $p= 0.83$, $\eta_p^2 = 0.00$) but a main effect of probability ($F(1,40)= 6.83$, $p= 0.013$, $\eta_p^2 = 0.15$) on the SSM parameter *b*. Different from the

adaptation, the parameter *a* in SSM fitting of re-adaptation data showed a main effect of probability ($F(1,40)= 6.18$, $p= 0.017$, $\eta_p^2 = 0.13$) and the main effect of incentive approached significance ($F(1,40)= 3.73$, $p= 0.06$, $\eta_p^2 = 0.08$). There was no significant interaction ($F(1,40)= 1.04$, $p= 0.31$, $\eta_p^2 = 0.02$). Tukey HSD post-hoc comparison revealed significant difference in the SSM parameter *a* between 50%-Reward and 100%-Punishment groups (mean difference= 0.49, p= 0.017).

Adaptation Phase compared to Re-adaptation Phase as a Measure of Savings

Similar as in Morehead et al. (2015) and Zarahn et al. (2008), savings was indicated by significant increase of the rate parameter *b* in the exponential fitting of adaptation error to the fitting of re-adaptation error. Fig. 6 shows the savings in the four experimental groups. The 100%-Reward group and the 50%-Punishment group showed marked increase of rate from adaptation to re-adaptation, but the 50%-Reward group and the 100%-Punishment group showed limited increase of rate. Since evident difference of adaptation parameter *b* among the four groups, a paired-sample t test was administered to test the change of parameter *b* from adaptation to re-adaptation (Huang et al. 2011). The 100%-Reward group showed savings as indicated by significant increase of rate from adaptation to re-adaptation ($t(10)= -1.90$, $p= 0.043$, $d= 0.80$). The 50%-Punishment group also had savings ($t(10)= -2.67$, $p= 0.011$, $d= 1.10$). The 50%-Reward group and the 100%-Punishment group showed no savings ($t(10)= -0.23$. $p= 0.41$, $d= 0.11$; $t(10)= -0.26$, $p= 0.40$, $d= 0.15$).

Savings could also be reflected by significant increase of heading angle from the first 15 adaptation trials to the first 15 re-adaptation trials (Morehead et al. 2015). The results are consistent with the results from exponential fitting. Specifically, the 100%-Reward group and the 50%-Punishment group showed savings ($t(10)= 4.08$, $p= 0.001$, $d= 1.59$; $t(10)= 3.68$, $p= 0.002$, $d= 0.96$) but the 50%-Reward group and the 100%-Punishment group had no savings ($t(10)= 1.47$, $p= 0.09$, $d= 0.57$; $t(10)= 1.20$, $p= 0.13$, $d= 0.39$).

Reaction time (RT) and Movement time (MT) within all Phases

Table 3 shows RTs and MTs of all phases in the four experimental groups. Mixed effects ANOVA with phase as a repeated factor was adopted to test RT and MT group differences. RT showed no main effects of incentive ($F(1,200)= 0.39$, $p= 0.53$, $\eta_p^2 = 0.002$) and probability ($F(1,200)= 0.15$, $p= 0.70$, $\eta_p^2 = 0.001$), and no significant interactions (incentive by probability $F(1,200)= 0.26$, $p= 0.61$, $\eta_p^2 = 0.001$; incentive by phase $F(4,200)= 0.12$, $p= 0.98$, $\eta_p^2 = 0.002$; probability by phase $F(4,200)= 0.12$, $p= 0.97$, $\eta_p^2 = 0.002$; incentive by probability by phase $F(4,200)= 0.42$, $p= 0.79$, $\eta_p^2 = 0.008$), but had a main effect of phase ($F(4,200)= 5.29$, $p< 0.001$, $\eta_p^2 = 0.10$). Tukey HSD post-hoc comparison showed No-vision phase had longer RT than baseline (mean difference= 0.039s, $p= 0.01$), adaptation (mean difference= 0.042s, $p= 0.005$), washout (mean difference= 0.046s, $p= 0.002$), and re-adaptation (mean difference= 0.049s, $p= 0.001$) phases.

MT showed no main effects of incentive (F(1,200)= 0.36, p= 0.55, $\eta_p^2 = 0.002$) and probability (F(1,200)= 0.00, p= 0.99, $\eta_p^2 = 0.000$), and no significant interactions (incentive by probability F(1,200)= 1.32, p= 0.25, $\eta_p^2 = 0.007$; incentive by phase F(4,200)= 0.49, p= 0.74, $\eta_p^2 = 0.10$; probability by phase F(4,200)= 0.97, p= 0.42, $\eta_p^2 = 0.02$; incentive by probability by phase F(4,200)= 0.59, p= 0.67, $\eta_p^2 = 0.01$), but had a main effect of phase (F(4,200)= 18.37, p< 0.001, $\eta_p^2 = 0.27$). Tukey HSD post-hoc comparison showed adaptation had longer MT than baseline (mean difference= 0.074s, p< 0.001), washout (mean difference= 0.096s, p< 0.001), and re-adaptation (mean difference= 0.071s, p< 0.001) but a comparable MT to the no-vision phase (mean difference= 0.027s, p= 0.22); no-vision had longer MT than baseline (mean difference= 0.047s, p= 0.003), washout (mean difference= 0.069s, p< 0.001), and re-adaptation (mean difference= 0.044s, p= 0.005) but a comparable MT to adaptation phase (mean difference= -0.027s, p= 0.22).

Discussion

The purpose of the present study was to examine how the probability of reward and punishment distribution modulates the effects of reward and punishment on visuomotor adaptation and consolidation of the adaptation memory. Four groups of young healthy participants were trained to adapt to an abrupt 50° CW visual cursor rotation under the influence of performance-based monetary reward or punishment feedback. Reward and punishment were distributed in 100% of the adaptation trials or in 50% of randomly selected adaptation trials. The present study replicated previous finding that punishment induced faster visuomotor adaptation (Galea et al. 2015),

showed that reward enhanced offline consolidation of visuomotor adaptation memory as indicated by savings, and extended our understanding how the probability of monetary reward and punishment distribution modulates the effects of reward and punishment on motor adaptation and consolidation of the adaptation memory.

As hypothesized, when provided with reward or punishment in 100% of the adaptation trials, punished participants adapted much faster than rewarded participants. This is consistent with the findings of Galea et al. (2015), in which punished participants adapted much faster compared to rewarded participants when they adapted to an abrupt 30° CCW rotation to reach a single target or eight targets. In a serial reaction time task, Wächter et al. (2009) and Steel et al. (2016) also showed faster learning in punished participants compared to rewarded participants.

Hypothesis 2, that 50% compared to 100% reward and punishment would result in better consolidation, was partially supported. Comparing the completely (100%) rewarded group and the partially (50%) rewarded group, the two groups adapted comparably to the same visual rotation, but the completely rewarded group showed savings when re-adapting to the same visual rotation, showing that 100% rewarded trials resulted in offline consolidation improvement, which is opposite findings than were expected. Comparing the completely (100%) punished group and the partially (50%) punished group, the completely punished group adapted significantly faster but the partially punished group showed savings, which is consistent with the hypothesis. The finding that the completely rewarded group showed offline consolidation gain

expressed as savings is consistent with the result of Abe et al. (2011). However, Steel et al. (2016) found no benefit of reward to offline consolidation of motor memories tested with a serial reaction time task and a force-tracking task. Factors such as motor task, feedback protocol, and training procedure may influence the effect of reward on consolidation of motor memory.

There are several possibilities for the distinct effects of reward and punishment on visuomotor adaptation. As proposed by Galea and colleagues (2015), punishment may induce the cerebellum to be more sensitive to sensory prediction errors, which are the differences between the predicted location and the perceived location of the cursor. Sensory prediction error was thought to be a main driving factor in motor adaptation (Tseng et al. 2007), and the cerebellum was probably involved in its encoding (Schlerf et al. 2012). The cerebellum was also found to encode aversive stimuli (Moulton et al. 2011) and to be sensitive to negative emotions (Sacchetti et al. 2009). Hence, it is possible that punishment may enhance the sensitivity of the cerebellum to sensory prediction errors. This possibility is also in agreement with the finding in the current study that partially (50%) punished participants adapted much slower than completely (100%) punished participants but partially (50%) rewarded participants adapted comparably with completely (100%) rewarded participants. When participants were punished only in 50% of randomly selected adaptation trials, punishment was unpredictable, and the decrease of sensory prediction error would not certainly reduce punishment. In contrast, when participants were punished in 100% of adaptation trials, punishment was predictable. So to reduce punishment, performance had to be improved,

resulting in decreased sensory prediction errors. Hence it is possible that punishment prompts completely punished participants to be more sensitive to sensory prediction errors so to reduce punishment.

If punishment and reward induce different cerebellar sensitivity to sensory prediction errors, participants may show differences in after-effects when the visual rotation is removed in the washout phase. After-effects are thought to reflect implicit learning (Buch et al. 2003). However, in the current study, the completely and partially rewarded and punished groups had comparable after-effects. Thus, these results suggest another possible explanation.

Another explanation for differences in adaptation induced by punishment and reward is that punished participants and rewarded participants may have similar implicit learning but employ different cognitive strategies. Consistent with this interpretation, Mazzoni and Krakauer (2006) instructed a group of participants to use a cognitive strategy to adapt to a 45° CCW cursor rotation. Compared to the control group without explicit instruction of any cognitive strategy, the cognitive strategy group initially adapted much faster to the rotation, but the two groups showed very similar after-effects in the washout phase. According to their findings, the explicit strategy did not alter the implicit learning process but changed the adaptation process.

In the present study, punished participants may have formed a more efficient cognitive strategy so to minimize punishment due to greater sensitivity to losses, which has been extensively demonstrated to influence human's behavior robustly (for review

see Barberis 2013). When receiving punishment or reward in the adaptation phase, participants had to make decisions based on previous outcomes to continue the previously executed action or to switch to a different action on the next trial. This win-stay/lose-shift strategy has been demonstrated to be an effective strategy in this type of choice behavior (Worthy et al. 2012; Imhof et al. 2007). Participants would stay with the same option on the next trial if they were rewarded or switch to a different option on the next trial if they were punished. This may have driven punished participants to explore different strategies and quickly discover the optimal strategy to adapt and not to get punished. In constrast, rewarded participants may have been deferred to search the optimal strategy to adapt since they could still get rewarded even if they stayed with imperfect reaching. This explanation is supported by the results in the analysis of trial-by-trial change of heading angle. When participants received punishment or reward feedback in all the adaptation trials, the 100%-Punishment group showed significantly greater trial-by-trial increase of heading angle after receiving big loss than the 100%-Reward group after receiving small gain, indicating that big loss was more effective to drive participants to increase heading angle to the right direction and thus induce faster adaptation than small gain, likely due to greater sensitivity to big loss than to small gain. When participants received punishment or reward feedback only in 50% randomly selected adaptation trials, although the 50%-Punishment group also showed greater trial-by-trial increase of heading angle after receiving big loss than the 50%-Reward group after receiving small gain, the difference of trial-by-trial change between the two groups was not significant. This insignificant difference was likely due to reduced

sensitivity to big loss in the 50%-Punishment group and it is also consistent with the result that the 50%-Punishment group adapted much slower than the 100%-Punishment group. These results on trial-by-trial analysis potentially indicate that big loss and small gain may act as negative motivational feedback that seems be a powerful inducer to improve performance immediately, and further that punishment has the bigger effect than reward. Given the dramatic performance change in initial phase of adaptation in the 100%-punishment group, it is possible that negative drive from big loss may stimulate completely punished participants to promptly search for the optimal strategy.

Regarding difference in offline consolidation as measured by savings, a possible explanation for the different effects of reward and punishment is that punishment-induced memory may decay faster. In the current study, after washout of previous adaptation training, the completely (100%) rewarded group showed savings in re-adapting to the same rotation but the completely punished group showed no savings in re-adaptation. Stronger residual representation of initial learning could engender greater savings. The strength of this residual representation of initial learning could be affected by decay, interference (offline stabilization), and/or offline consolidation (Song 2009), and could be differently influenced by punishment and reward. Nakatani and colleagues (2009) found in sensory learning in crickets that sensory memory induced by punishment decayed much faster than that induced by reward, probably due to different neurotransimitters conveying punishment and reward. Human studies indicate punishment may be modulated by serotonin and reward by dopamine (Crockett et al. 2009). This biochemical difference may be an explanation for findings on savings.

Abe and colleagues (2011) found in implicit motor sequence learning that reward memory, compared to punishment memory, induced marked offline consolidation improvement at about 12 hours post initial training. Offline consolidation occurs immediately post practice, and its benefit is time-dependent (Song 2009). Brown and Robertson (2007) proposed that offline consolidation was influenced by the interaction of implicit and explicit motor memory systems, and the offline consolidation gain relied on disengagement of the competition between explicit and implicit memory. This proposal seemingly supports the current finding that partially (50%) punished participants showed savings but completely (100%) punished participants had no savings. Possibly due to loss aversion, completely punished participants had stronger explicit learning and memory, and thus stronger competition between explicit and implicit memory, which afterward constrained the offline consolidation of punishment-induced memory in the completely punished group.

Different from Dayan et al. (2014), the 50%-Reward group in the present study showed no savings in re-adaptation but the 100%-Reward group induced savings. The following factors may have resulted in this inconsistency. Firstly, the experimental tasks and performance measures were different. In Dayan et al. the experimental task was a sequentially timed force production task and the performance measure was an index based on movement time and error. In the present study, the experimental task was a visuomotor adaptation task and the performance measure was based on heading angle. Secondly, the rewarding protocols were different. Dayan et al. used binary reward determined by movement time and the reward magnitude was different among

probability groups. The present study used gradient reward determined by error and the reward magnitude was the same among groups. Although the 50%-Reward group received comparable money due to extra $5 added, the average amount of money the group won ($4.0±1.9) in the adaptation phase was much less than that in the 100%-Reward group ($9.3±2.5). This may have constrained the effect of reward on offline consolidation in the 50%-Reward group.

Inconsistent with Galea et al. (2015), the present study did not show retention difference measured by the no-vision phase among the four experimental groups. Except for decline in the beginning of the no-vision phase, heading angles in all the four groups did not decay with the passage of time. However, Galea and colleagues found remarkable decay of heading angle in the punished group. This inconsistency is probably due to the difference between the experimental settings and instructions in the adaptation phase in the two studies. Firstly, the visual rotation applied is different, the present study applied a 50° CW rotation but the Galea study used a 30° CCW rotation. Morehead et al. (2015) reported that adapting to a 30° rotation did not show savings but adapting to a 60° rotation showed marked savings. This suggests that the retention of the 30° adaptation memory may be different from that of the 50° adaptation memory. Secondly, the adaptation and no-vision phase had the same visual context in the present study, this may also lead to no decay of motor memory. Vaswani and Shadmehr (2013) found no decay of dynamic motor adaptation in error clamp trials (in which errors were absent) if movements and contexts were made similar as in the perturbation phase and participants did not detect a change in task conditions. Besides, in the current study

participants in all the four groups showed significantly longer reaction time in the no-vision phase than in other phases but the Galea study reported comparable reaction time across phases. This indicates participants in the current study may involve more cognitive preparation so to carry out the reaching in the context of no visual feedback of the cursor (except in the start square). The preparation may involve deeper recall of previous adaptation training and thus hinder decay of the adaptation memory.

Conclusion

In summary, by manipulating probability of distribution, the present study demonstrated the distinct effects of reward and punishment on visuomotor adaptation. Participants punished in 100% of the adaptation trials rapidly adapted to the visual rotation but did not show savings in re-adaptation. In contrast, participants punished in 50% of the adaptation trials and participants rewarded in 100% of the adaptation trials adapted slowly but had marked savings in re-adaptation. It is still not clear what caused the distinct effects of reward and punishment on visuomotor adaptation and consolidation of the adaptation memory, but sensitivity to sensory prediction error or difference in explicit learning induced by reward and punishment may likely contribute to the distinct effects of reward and punishment.

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Conflict of Interest

The authors declare that they have no financial disclosures or potential conflicts of interests.

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Table 1. Group mean fit parameter values of SSM

	50%-Reward	100%-Reward	50%-Punishment	100%-Punishment
Adaptation				
A	0.79±0.08	0.71±0.09	0.71±0.10	0.62±0.06
B	0.08±0.03	0.07±0.02**	0.06±0.03**	0.18±0.04
RMS	8.71±0.80	12.34±1.48	12.37±1.41	9.14±1.01
Re-adaptation				
A	0.62±0.14*	0.23±0.09	0.29±0.12	0.13±0.09
B	0.19±0.07*	0.30±0.05	0.24±0.06	0.39±0.04
RMS	8.38±1.22	9.69±1.38	10.01±1.20	9.25±1.11

Data represents means ± s.e. * represents $p<0.05$ and ** represents $p<0.01$, compared to 100%-Punishment group.

Table 2. Group mean heading angle (°) of pre-selected trials

	50%-Reward	100%-Reward	50%-Punishment	100%-Punishment
Baseline				
Last-15	3.88±0.56	2.70±0.36	2.70±0.26	3.12±0.19
Adaptation				
First-15	12.2±2.72	7.51±4.98**	9.28±5.04**	26.83±2.78
Last-15	30.00±3.60	34.86±3.11	27.15±5.16	40.00±1.32
No-vision				
First-15	21.64±2.61	25.90±3.16	21.03±2.52	28.65±3.68
Last-15	23.21±3.87	22.62±4.89	22.14±2.42	30.33±2.55
Washout				
First-15	11.40±1.47	8.23±1.70	13.50±3.16	9.73±1.57
Last-15	6.44±1.03	4.59±0.96	4.83±0.82	4.47±0.48
Re-adaptation				
First-15	19.47±5.06	30.69±4.06	24.36±4.76	32.83±6.25

Data represents means ± s.e. * represents $p<0.05$ and ** represents $p<0.01$, compared to 100%-Punishment group.

Table 3. Group means of RT and MT in each phase

	50%-Reward	100%-Reward	50%-Punishment	100%-Punishment	Average
Baseline					
RT(ms)	342±12	318±13	321±11	339±30	330±9
MT(ms)	366±10	351±8	341±12	358±18	354±6
Adaptation					
RT(ms)	329±11	326±10	338±15	316±16	327±6
MT(ms)	437±18	441±32	392±23	443±19	428±12**
No-vision					
RT(ms)	373±14	368±12	370±18	368±32	370±10*
MT(ms)	408±37	404±23	408±22	385±25	401±13**
Washout					
RT(ms)	330±14	326±11	314±17	325±24	324±8
MT(ms)	339±8	322±9	344±9	323±10	332±5
Re-adaptation					
RT(ms)	327±21	328±10	314±16	314±23	321±9
MT(ms)	358±12	344±16	352±10	373±9	357±6

Data represents means ± s.e. * represents $p<0.05$ and ** represents $p<0.01$ across phases. No significant differences across groups.

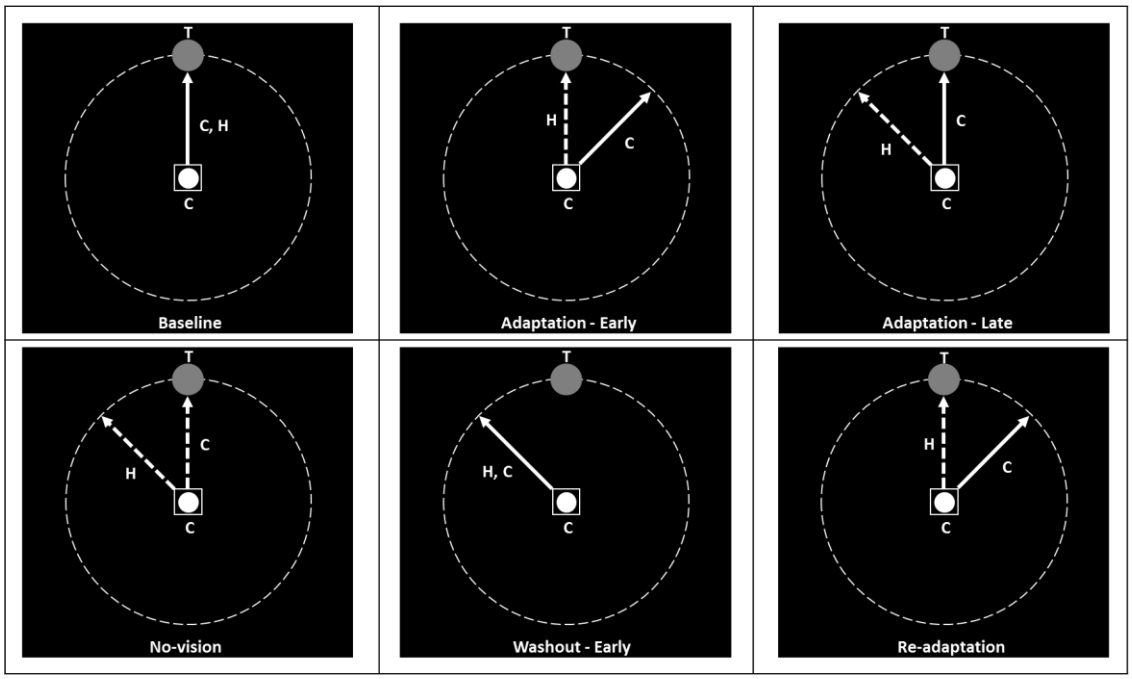


Fig. 1 Test conditions. Each frame shows the start square with the white cursor inside, the cursor and the heading direction of the cursor (C) dashed or solid arrows (dashed arrow means no visual feedback of the cursor, solid arrow means continuous visual feedback of the cursor), the target (T), the invisible circular boundary (dashed circle, not displayed on the monitor), and the heading direction of the hand (H) (dashed arrow, direct vision of the hand was blocked).

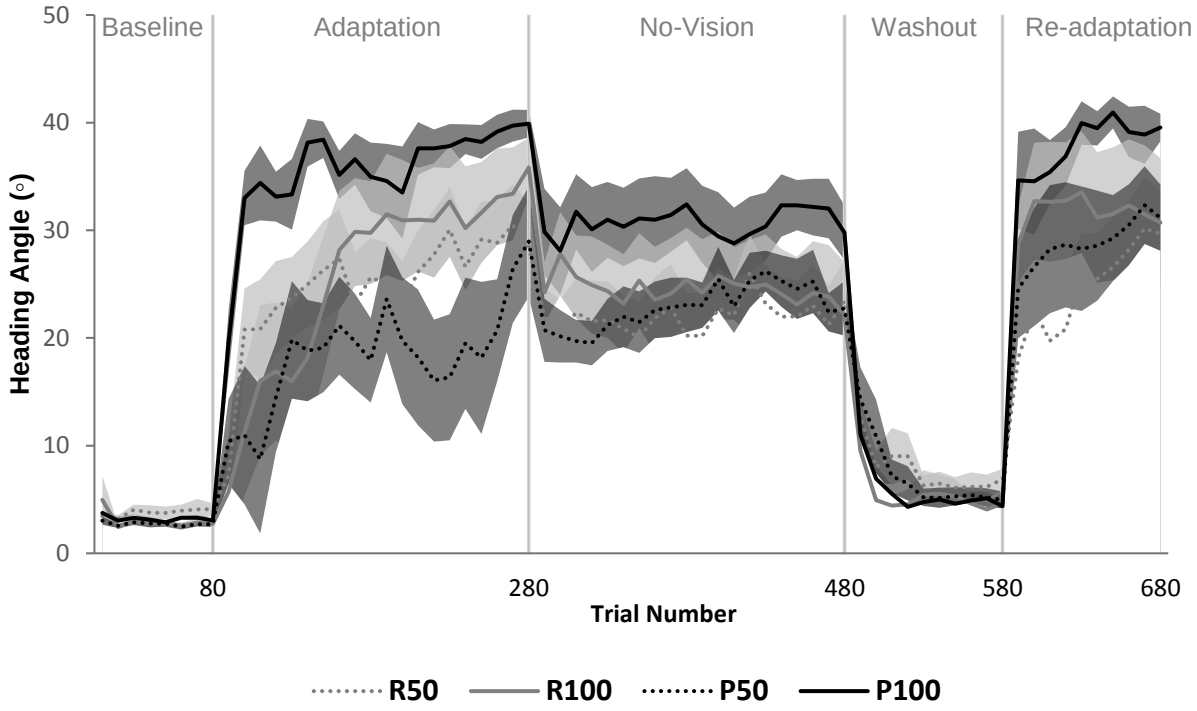
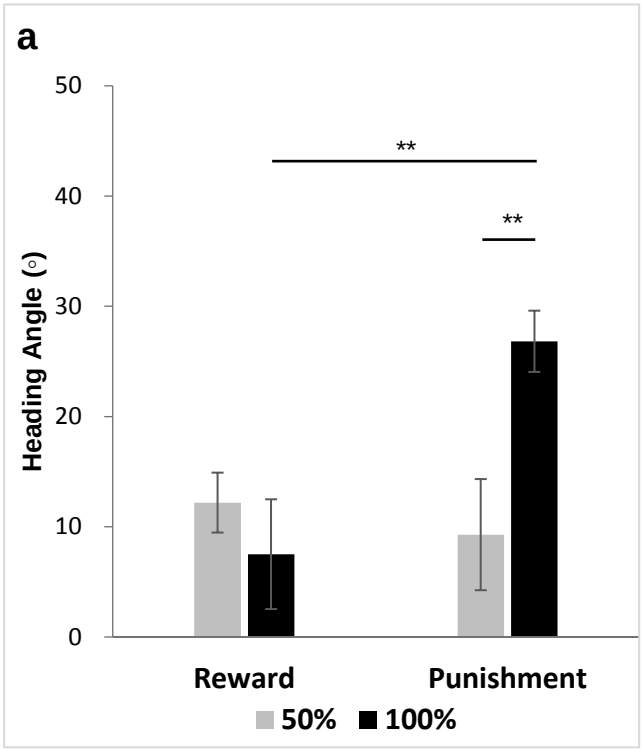


Fig. 2 Bin (averaged across ten trials) heading angle data for the four experimental groups, shaded area represents confidence interval around the mean.



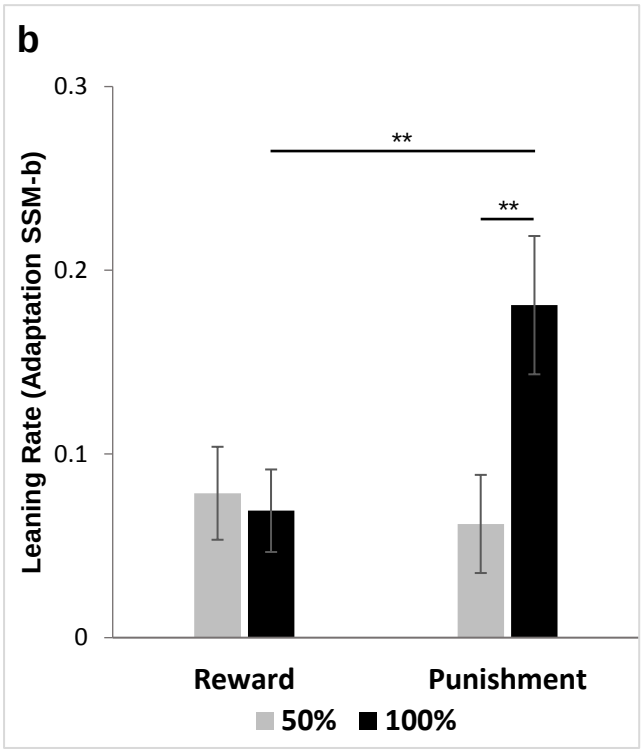
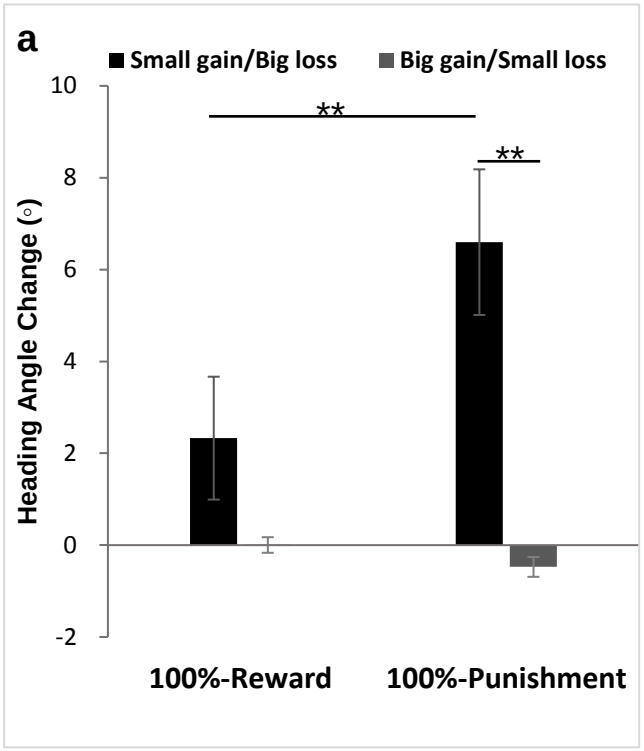


Fig. 3 a. Mean heading angle of the first 15 adaptation trials in each group; b. Learning rate assessed by the mean of parameter b in the SSM model fitting of all adaptation trials in each group. Error bars represent standard errors. * represents $p < 0.05$; ** represents $p < 0.01$.



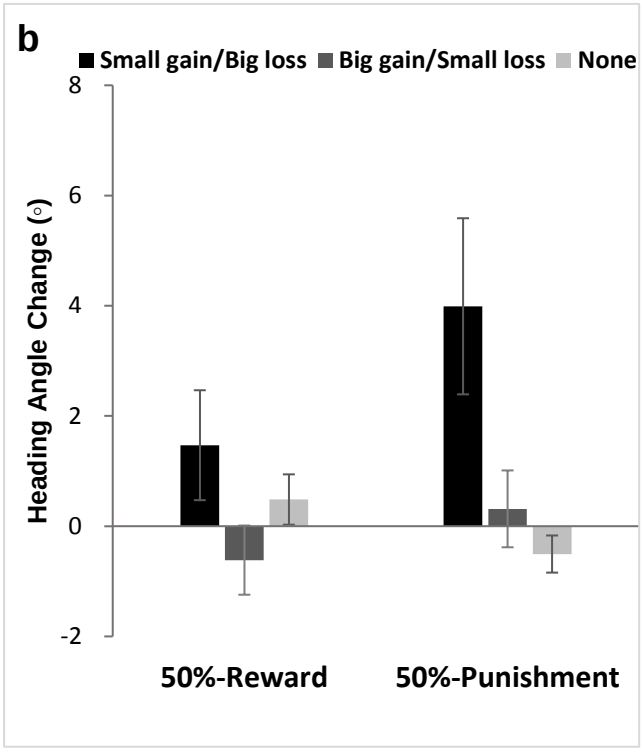


Fig. 4 a. Trial-by-trial change of performance error after receiving small gain or big gain and small loss or big loss in the 100%-Reward group and the 100%-Punishment group; b. Trial-by-trial change of performance error after receiving small gain or big gain and small loss or big loss and no incentive feedback in the 50%-Reward group and the 50%-Punishment group. Small gain: 0¢, +1¢, +2¢, +3¢; big gain: +4¢, +5¢, +6¢, +7¢; big loss: -7¢, -6¢, -5¢, -4¢; small loss: -3¢, -2¢, -1¢, 0¢; none: =. Error bars represent standard errors. * represents $p < 0.05$; ** represents $p < 0.01$.

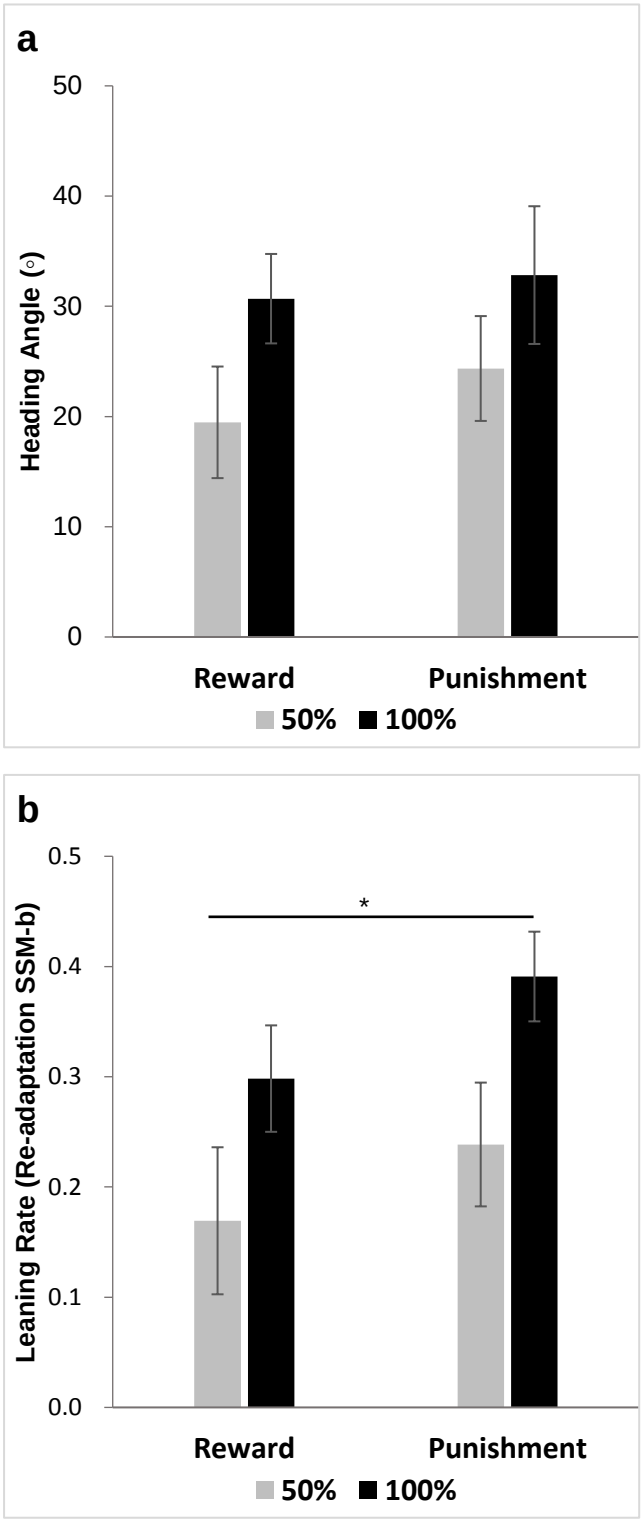


Fig. 5 a. Mean heading angle of the first 15 re-adaptation trials in each group; b. Learning rate assessed by the mean of parameter b in the SSM model fitting of all re-adaptation trials in each group. Error bars represent standard errors. * represents $p < 0.05$; ** represents $p < 0.01$.

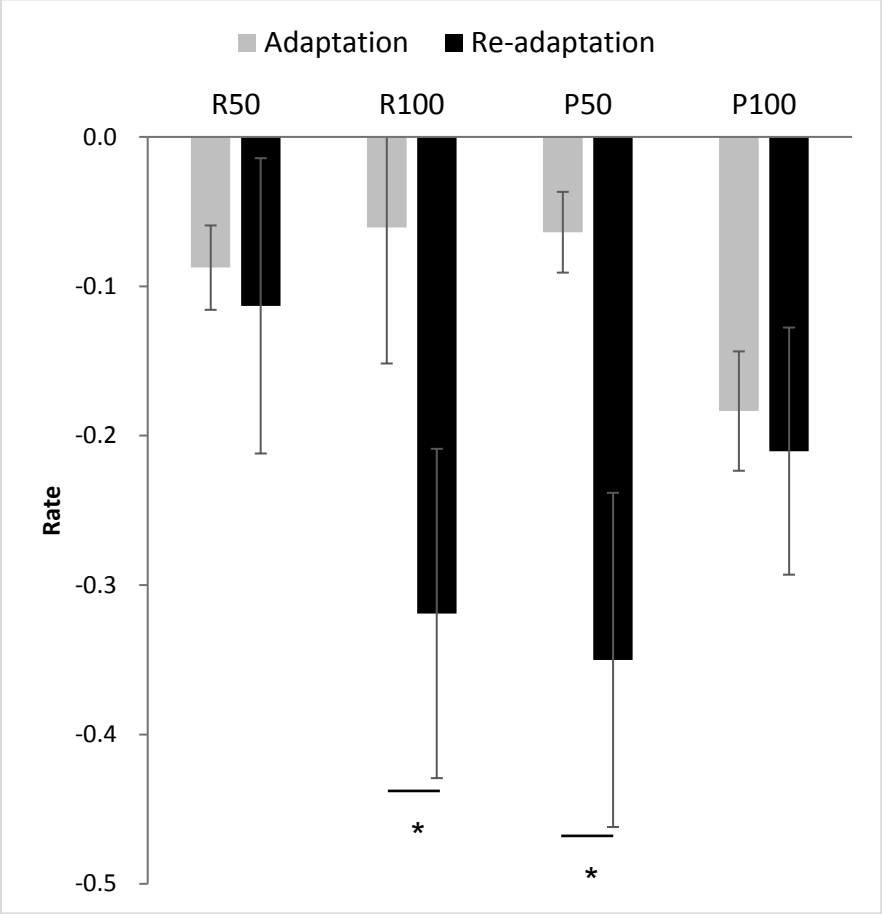


Fig. 6. Savings assessed by rate in exponential fitting of the first 60 adaptation trials and fitting of the first 60 re-adaptation trials. Error bars represent standard errors. * represents $p < 0.05$; ** represents $p < 0.01$.

Appendix – IRB Approval

IOWA STATE UNIVERSITY
OF SCIENCE AND TECHNOLOGY

Institutional Review Board
Office for Responsible Research
Vice President for Research
1138 Pearson Hall
Ames, Iowa 50011-2207
515 294-4566
FAX 515 294-4267

Date: 2/4/2016

To: Yanlong Song
283 Forker

From: Office for Responsible Research

Title: Modulating Visuomotor Adaptation: The Effects of Reward, Penalty, and Dopamine

IRB ID: 15-754

Approval Date:	2/4/2016	**Date for Continuing Review:**	1/15/2017
Submission Type:	New	**Review Type:**	Full Committee

The project referenced above has received approval from the Institutional Review Board (IRB) at Iowa State University according to the dates shown above. Please refer to the IRB ID number shown above in all correspondence regarding this study.

To ensure compliance with federal regulations (45 CFR 46 & 21 CFR 56), please be sure to:

Use only the approved study materials in your research, **including the recruitment materials and informed consent documents that have the IRB approval stamp.**

Retain signed informed consent documents for 3 years after the close of the study, when documented consent is required.

Obtain IRB approval prior to implementing any changes to the study by submitting a Modification Form for Non-Exempt Research or Amendment for Personnel Changes form, as necessary.

Immediately inform the IRB of (1) all serious and/or unexpected adverse experiences involving risks to subjects or others; and (2) **any other unanticipated problems involving risks** to subjects or others.

Stop all research activity if IRB approval lapses, unless continuation is necessary to prevent harm to research participants. Research activity can resume once IRB approval is reestablished.

Complete a new continuing review form at least three to four weeks prior to the date for continuing review as noted above to provide sufficient time for the IRB to review and approve continuation of the study. We will send a courtesy reminder as this date approaches.

Please be aware that IRB approval means that you have met the requirements of federal regulations and ISU policies governing human subjects research. **Approval from other entities may also be needed.** For example, access to data from private records (e.g. student, medical, or employment records, etc.) that are protected by FERPA, HIPAA, or other confidentiality policies requires permission from the holders of those records. Similarly, for research conducted in institutions other than ISU (e.g., schools, other colleges or universities, medical facilities, companies, etc.), investigators must obtain permission from the institution(s) as required by their policies. **IRB approval in no way implies or guarantees that permission from these other entities will be granted.**

Upon completion of the project, please submit a Project Closure Form to the Office for Responsible Research, 1138 Pearson Hall, to officially close the project.

Please don't hesitate to contact us if you have questions or concerns at 515-294-4566 or IRB@iastate.edu.

CHAPTER 4. MONETARY INCENTIVE EFFECTS ON ACQUISITION AND CONSOLIDATION OF VISUOMOTOR ADAPTATION MEMORY

A paper submitted to Experimental Brain Research

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Abstract

Reward and punishment were revealed to have dissociable effects on acquisition and consolidation of motor memory. This study examined the influences of monetary reward and punishment on visuomotor adaptation memory, and tested a possible cause for this dissociation from the perspective of interaction between explicit process and implicit process underlying visuomotor adaptation. During adaptation to an abrupt visual rotation in reaching a visual target, young healthy participants were provided with performance-based monetary reward or punishment. In the context of non-continuous visual feedback emphasizing explicit process, punishment prompted faster adaptation than reward and it also showed comparable consolidation as reward. In the context of continuous visual feedback involving both explicit and implicit processes, punishment still induced faster adaptation but reward markedly promoted consolidation expressed as stronger proactive interference in adapting to an opposite visual rotation and greater savings in adapting to the same visual rotation the second time. Consolidation of punishment-induced visuomotor adaptation memory was inhibited. The inhibition was reduced when participants engaged in a word-list

learning task immediately after the visuomotor adaptation. In contrast, the word-list learning task had no influence on the consolidation of reward-induced visuomotor adaptation memory. These findings suggest that punishment, compared to reward, induced more efficient explicit process in the adaptation phase but the more efficient explicit process suppressed consolidation of the visuomotor adaptation memory.

Keywords: reward, punishment, visuomotor adaptation, explicit process, implicit process

Introduction

Reward and punishment have been demonstrated to show distinct influences on human acquisition and consolidation of motor memory. Specifically, punishment accelerates acquisition of motor memory (Steel, Silson, Stagg, & Baker, 2016; Galea, Mallia, Rothwell, & Diedrichsen, 2015; Wächter, Lungu, Liu, Willingham, & Ashe, 2009) and reward facilitates consolidation of motor memory (Galea et al., 2015; Abe et al., 2011; Wächter et al., 2009). Inconsistently, Steel et al. (2016) found no benefits of reward in consolidation of motor memory. This study provided further evidence on the distinct effects of reward and punishment on motor memories in two visuomotor adaptation tasks.

Visuomotor adaptation occurs when an external perturbation introduces a discrepancy between actual and expected sensory consequences of a movement. The difference between observed sensory feedback and expected movement consequence is

termed as sensory prediction error, which is thought to be a crucial factor driving visuomotor adaptation in an implicit and automatic way (Shadmehr, Smith, & Krakauer, 2010; Tseng, Diedrichsen, Krakauer, Shadmehr, & Bastian, 2007). Contrary to the view that motor adaptation was an implicit process and insensitive to incentive feedback, a couple of studies revealed that reward and punishment feedback altered visuomotor adaptation (Izawa & Shadmehr, 2011; Nikooyan & Ahmed, 2015; Galea et al., 2015). Moreover, incentive feedback showed generalization and sensorimotor remapping different from that induced by sensory feedback (Izawa et al., 2011), indicating that sensory and incentive feedback may drive visuomotor adaptation through different mechanisms.

It is not clear what causes the potentially distinct effects of reward and punishment on visuomotor adaptation. One possible cause for punishment-induced faster acquisition of visuomotor adaptation memory, per Galea et al. (2015), is punishment-increased sensitivity of the cerebellum to sensory prediction error, which also modulates implicit process in visuomotor adaptation (Taylor, Krakauer, & Ivry, 2014). However, this possibility is debatable considering that implicit process arising from sensory prediction errors is relatively rigid (Bond & Taylor, 2015), invariant for perturbations between 7.5° and 95°, dropped off for larger perturbations, and saturated somewhere between 5° and 15° (Morehead, Taylor, Parvi, & Ivry, 2017).

It is increasingly clear that visuomotor adaptation is not a unitary implicit process but involves both implicit and explicit processes (Taylor et al., 2014). Specifically,

implicit process is modulated by sensory prediction error and is slow and monotonic; explicit process is modulated by performance error or explicit strategy, and achieved by initially larger then smaller explorations of movement direction biased toward the correct solution (Taylor et al., 2014; McDougle, Ivry, & Taylor, 2016). Moreover, the implicit process is invariant to the change of perturbation size (Morehead et al.,, 2017) but the explicit process shows positive correlation with the size of the perturbation (Bond & Taylor, 2015). The explicit process may be flexible to allow a mover to find good-enough or optimal solutions to achieve functional performance as the implicit process slowly and subtly homes in on the precise dynamics (McDougle et al., 2016).

Explicit process may not only influence online motor adaptation but also offline consolidation of motor adaptation memory. Poldrack and Packard (2003) reviewed findings from animal studies and concluded that multiple memory systems were activated simultaneously in various learning tasks and interaction between some memory systems, such as medial temporal lobe and basal ganglia memory systems, was competitive in nature. Brown and Robertson (2007) found that a word-list learning task immediately after an motor sequence training improved the 12-hour-late retention performance of the motor sequence. They thought that the offline gain was due to that the word-list learning introduced competitive declarative memory interfering or suppressing the explicit component of the motor sequence memory. The researchers proposed that offline motor memory consolidation relied on the disengagement of competition between explicit and implicit motor memory systems.

Keisler and Shadmehr (2010) further demonstrated that offline consolidation of motor adaptation memory was affected by competition between explicit and implicit motor memory systems in a series of force field motor adaptation experiments through controlling the amount of training. They found that a word-pair learning task did not change the consolidation of motor adaptation memory formed after extended training (implicit memory). On the contrary, following short training, the word-pair learning task altered the consolidation of motor adaptation memory, which involved both explicit and implicit motor memory components so the word-pair learning task probably suppressed consolidation of the explicit component and improved consolidation of the implicit component of motor adaptation memory.

All these findings support the interactive influence of explicit and implicit processes during motor adaptation (Taylor et al., 2014; McDougle et al., 2016) and the offline consolidation of motor memory (Brown et al., 2007; Keisler et al., 2010). Explicit and implicit processes may function in synergy to drive online motor adaptation, but the explicit component of motor adaption memory may compete with the implicit component of motor adaptation memory to influence offline consolidation and expression of motor adaptation memory.

As to the distinct effects of punishment and reward on motor memory, it is possible that punishment and reward may induce different explicit process. To test this possibility, we applied two visuomotor adaptation tasks in this work. Based on the evidence that explicit process is flexible and implicit process is rigid (Mazzoni &

Krakauer, 2006; Bond et al., 2015; Morehead et al., 2017), we hypothesized that punishment, compared to reward, would induce more efficient explicit process or strategy use during adaptation to an abrupt visual rotation. More efficient explicit process should contribute to faster visuomotor adaptation in participants who receive punishment, but the stronger explicit process should in turn inhibit offline consolidation of punishment-induced visuomotor adaptation memory.

Two experiements were designed to test this hypothesis. In the first experiment, continuous visual feedback of the cursor was withheld and only performance-based reward or punishment feedback was provided at the end of an adaptation trial so that explicit process was primarily underlying the visuomotor adaptation (Butcher & Taylor, 2017; (Christou, Miall, Mcnab, & Galea, 2016; Izawa et al., 2011). If punishment induced more efficient explicit process compared to reward, then punishment should induce faster adaptation. Since this training protocol primarily produced explicit motor memory (thus limited competition between explicit and implicit motor memory components), offline consolidation of punishment-induced visuomotor adaptation memory and reward-induced visuomotor adaptation memory should be comparable.

In the second experiment, continuous visual feedback of the cursor was provided in the adaptation phase so that both explicit and implicit process drive the visuomotor adaptation. We hypothesized if punishment induced more efficient explicit process compared to reward, then punishment should induce faster adaptation; correspondingly, punishment should also induce stronger explicit motor

memory component, which would compete with the implicit motor memory component and inhibit offline consolidation of punishment-induced visuomotor adaptation memory. This inhibition should be reduced by a declarative learning task (word-list learning) that was aimed to suppress the explicit motor memory component of the visuomotor adaptation memory (Brown & Robertson, 2007). In contrast, reward-induced visuomotor adaptation memory should have weak competition from the explicit motor memory component and the declarative learning task should not influence the offline consolidation of reward-induced adaptation memory.

Method

Participants

Seventy-two undergraduate students participated in the two experiments in this study. Participants were recruited through email advertisement. The mean age of participants was 20.1 years (range 18-30, SD 1.8, 36 females). All participants reported having normal health conditions and they were required to be right-handed, which was also checked with Edinburgh Handedness Inventory (Oldfield, 1971). The study was approved by the University Institute Review Board. Before participation, all participants provided their informed consent.

Apparatus

Participants performed a center-out fast reaching movement by controlling a virtual cursor displayed on the computer monitor of a desktop computer (Dell). The computer monitor was 37.5 cm wide, 30.5 cm high, had a resolution of 1024 by 768

pixels, and it was placed vertically and 50 cm away from participants' foreheads. Participants were seated in an arm chair with the chair height adjusted such that their eyes were level with the center of the monitor. They held a stylus pen and slid the pen on a digitizing tablet (Wacom) to control the moving of the cursor. Direct vision of their hands was blocked by a level surface before the monitor. The display was controlled by software (Mathworks) from the desktop computer to display a white-edge start square (5 mm by 5 mm), a white circular cursor (3 mm diameter), and a circular target (6 mm diameter) in a black full-screen window. The start square was fixed at the center of the monitor and was displayed throughout the experiment. The target was displayed vertically above (90° direction) and 10 cm away from the start square.

Task

Fig.1A is a schematic illustration of the experimental task. When participants moved the cursor into the center of the start square, the target appeared in red and after a randomly-generated period ranging from 1 to 2s, the target changed to green. Participants were instructed to move the cursor to hit the target once the target changed to green. To control the influence of error correction, participants were instructed to move the cursor through the target in a non-curving way, not to correct the moving trajectory of the cursor, and not to stop the cursor on the target. After the center of the cursor moved beyond the invisible circular boundary where the center of the target was located, both the cursor and the target disappeared. An auditory

feedback of “too fast” or “too slow” was played if the movement time of the cursor was less than 200ms or more than 700ms. Before moving the cursor back to the start square, participants were instructed to pause to make the moving-out and moving-in of the cursor discontinuous.

Experiment 1

Thirty-two participants were randomly assigned into two groups, 16 in each group. Fig. 1B illustrates the test conditions in Experiment 1. It consisted of 80 baseline trials, 300 adaptation trials, 100 washout trials, and 60 re-adaptation trials. In the baseline phase and washout phase, movement of the cursor was congruent with the movement of the pen, and continuous visual feedback of the cursor was provided. In the adaptation and re-adaptation phases, the movement of the cursor was rotated by 50° counter clockwise (CCW) relative to the movement of the pen, and the cursor was only displayed when it was in the start square. In the adaptation phase, participants won or lost money in each trial. When the cursor moved outside the invisible circular boundary, the target disappeared and the amount of money a participant won or lost from that adaptation trial was displayed above the target position in a two-significant-digit decimal number with the “+” or “-” sign in red and in 48 font size for 1s. Since continuous visual feedback of the cursor was not provided, participants had to plan the next movement based on the monetary feedback in previous trials. Hence the adaptation was driven by explicit learning. In the re-adaptation phase, when the cursor moved outside the invisible circular boundary, the target disappeared and a “Hit” or

"Miss" was displayed above the target position in red and in 48 font size for 1s. The "Hit" was displayed if the absolute value of performance error (the angular distance from the cursor to the target when the cursor moved through the invisible circular boundary) was within 0° to 2°. The "Miss" was displayed if the absolute value of performance error was larger than 2°. The rest interval between phases was one minute.

Participants in each group were provided with monetary incentives in the adaptation phase. The reward group won money in every adaptation trial. The punishment group lost money in every adaptation trial. In the beginning of the adaptation phase, the punishment group was provided with 15 dollars, and they lost money from 0 to 5 cents in each adaptation trial. The reward group won money from 0 to 5 cents in each adaptation trial. How much money a participant won or lost from an adaptation trial when absolute performance error was smaller than 50° was determined by the performance error according to the following rule:

$$\text{Reward: } 5\times\frac{50-|performance\ error|}{50}$$

$$\text{Punishment: } 5\times\frac{50-|performance\ error|}{50}-5$$

If absolute performance error was bigger than 50°, the reward group won zero cent and the punishment group lost five cents. Participants were instructed that the amount of money one could win or lose in an adaptation trial was determined by the accuracy of the cursor hitting the target, and they were encouraged to try their best to maximize the money they could win or minimize the money they could lose.

Experiment 2

Forty participants were randomly assigned into four groups, 10 in each group. Fig. 1C illustrates the test conditions in Experiment 2. It consisted of 80 baseline trials, 100 adaptation trials, word-list learning or rest in the lab for 30 minutes, 15 de-adaptation trials, a six-hour interval out the lab in which participants were asked not to take naps, and 60 re-adaptation trials. Continuous visual feedback of the cursor was provided in all phases. In the baseline phase, movement of the cursor was congruent with the movement of the pen. In the adaptation and re-adaptation phases, the movement of the cursor was rotated by 50° clockwise (CW) relative to the movement of the pen. In the de-adaptation phase, the movement of the cursor was rotated in the opposite direction by 50° CCW. In the adaptation phase, participants won or lost money in each trial. When the cursor moved outside the invisible circular boundary, the target and the cursor disappeared and the amount of money a participant won or lost from that adaptation trial was displayed above the target position in a two-significant-digit decimal number with the "+" or "-" sign in red and in 48 font size for 1s. Since continuous visual feedback of the cursor was provided, the adaptation was driven by explicit and implicit learning (Taylor et al. 2014).

Immediately after the adaptation phase, some participants were asked to learn a list of 16 English nouns in four categories for 30 minutes, and some participants were asked to take a break to rest in the lab for 30 minutes doing nothing but sitting and resting. The word-list learning was organized in reference to the California

Verbal Learning Test (CVLT) (Delis et al. 1987). Specifically, a word in the word list was displayed on the center of the computer monitor for 3s with the order of words fixed. After displaying of all words from the list, participants were asked to speak out the words they could remember from the list in any order. This process was repeated four more times. After the last round of practice, participants were asked to take a 15 minute break to rest, and they were also explicitly informed that they would be asked to write down the words they could remember from the list after the break. Then after the 15 minute break, participants wrote down the words they could remember in any order. After the 30-minute interval, all participants completed 15 trials of de-adaptation. Then they left the lab and came back after 6 hours to do the re-adaptation. After the re-adaptation, participants who learned the word-list were asked to write down the words they could remember from the list for the second time. They were not informed about this second word recall test before they left the lab.

Participants in each group were provided with monetary incentives in the adaptation phase. The two reward groups won money in every adaptation trial. The two punishment groups lost money in every adaptation trial. In the beginning of the adaptation phase, the two punishment groups were provided with 12 dollars to begin, and then they lost money from 0 to 12 cents in an adaptation trial. The two reward groups won money from 0 to 12 cents in an adaptation trial. How much money a participant won or lost from an adaptation trial when absolute performance error was smaller than 50° was determined by the performance error according to the following rule:

$$\text{Reward: } 12\times\frac{50-|performance\ error|}{50}$$

$$\text{Punishment: } 12\times\frac{50-|performance\ error|}{50}-12$$

If absolute performance error was bigger than 50°, the two reward groups won zero cent and the punishment groups lost 12 cents. Participants were instructed that the amount of money one could win or lose in an adaptation trial was determined by the accuracy of the cursor hitting the target, and they were encouraged to try their best to maximize the money they could win or minimize the money they could lose. After the adaptation phase, one reward group and one punishment group learned the word list, and the other reward group and the other punishment group rested for 30 minutes.

Data Analysis

Performance error was the primary dependent variable and was used to assess adaptation performance and the consolidation of adaptation memory. The performance error was defined as the angular distance from the cursor to the target when the cursor moved through the invisible circular boundary. The calculation of performance errors was based on Cartesian X and Y coordinates of the cursor, which were sampled at 100 Hz. Data of each phase in the two experiments were blocked across 10 trials. Performance of each phase was based on mean performance error. Specifically, the last baseline block, the first and the last washout block, the first de-adaptation block, and the first re-adaptation block were selected to assess performance in corresponding phases in the two experiments. Adaptation performance was

assessed by block change of performance errors across all adaptation blocks. A main effect of block indicates adaptation occurred.

Trial-by-trial change of performance error was analyzed to assess how reward and punishment feedback influenced adaptation. The degree change of performance error on trial *t+1* after receiving a certain reward or punishment feedback on trial *t* was defined as the difference between performance error on trial *t+1* and performance error on trial *t* (Chen et al. 2017). To measure how the magnitude of reward or punishment feedback influenced the effects of reward or punishment on adaptation, reward feedback was categorized into small gain and big gain, and punishment feedback was categorized into big loss and small loss. Specifically, in *Experiment 1*, small gain was operationalized as reward feedback smaller than +2¢ and down to 0¢, big gain was operationalized as reward feedback equal and greater than +2¢ and up to +5¢, big loss was operationalized as punishment feedback equal and smaller than -2¢ and down to -5¢, small loss was operationalized as punishment feedback greater than -2¢ and up to 0¢. In *Experiment 2*, small gain was operationalized as reward feedback smaller than +5¢ and down to 0¢, big gain was operationalized as reward feedback equal and greater than +5¢ and up to +12¢, big loss was operationalized as punishment feedback equal and smaller than -5¢ and down to -12¢, small loss was operationalized as punishment feedback greater than -5¢ and up to 0¢. The mean of trial-by-trial change of performance error after receiving small gain or big gain and small loss or big loss was quantified in individual participant and further analyzed.

The two reward groups were collapsed as a reward group and the two punishment groups were collapsed as a punishment group in *Experiment 2*.

Adaptation data can also be fitted with a two-state state space model (SSM) as proposed by Smith et al. (2006) to infer the involvement of explicit and implicit learning in the adaptation process. They proposed fast and slow processes interactively contributed to motor adaptation. McDougle et al. (2015) demonstrated that explicit learning could be captured by the fast process but implicit learning could not be adequately described by the slow process. Albeit inadequately describing implicit learning, the two-state SSM can provide indirect estimation of explicit and implicit learning. The two-state SSM should produce a good fit of adaptation data in *Experiment 2* since the adaptation involves both explicit and implicit learning, but it should not have a good fit of adaptation data in *Experiment 1* for the adaptation was dominated by explicit learning. This was supported by a bad fit of adaptation data in *Experiment 1* and significant difference of goodness of fit between the two experiments. Hence the fitting results of *Experiment 1* were not further analyzed. Due to the inadequacy in describing implicit learning, the fitting results of *Experiment 2* were only used as reference data.

Savings was quantified as the difference between parameter *b* in the exponential fitting of the first 50 adaptation trials and fitting of the first 50 re-adaptation trials (Morehead et al. 2015; Zarahn et al. 2008). A positive difference

indicates savings occurred in re-adapting to the same rotation the second time. The exponential fitting function used is:

$$e_n = \mathrm{a}e^{bn} + c$$

where e_n is the performance error experienced at trial *n*. Parameter *a*, *b*, and *c* were estimated in the exponential fitting, *a* was thought to represent the range of error change from the beginning to the end of learning, *b* the learning rate, and *c* the asymptote value (Heathcote et al. 2000). The nonlinear least square method provided by Matlab was applied in the exponential fitting. The range for *b* was constrained from -1 to 1. The exponential fitting was applied to fit performance errors in the first 50 adaptation trials and the first 50 re-adaptation trials in each participant.

Performance error differences across phases were tested with mixed effects ANOVA with incentive as a between-subjects factor and block as a within-subjects factor in *Experiment 1*. Performance error differences in the adaptation phase were tested with a three-way mixed ANOVA with incentive and rest/word-list learning as two between-subjects factors and block as a within-subjects factor, and performance error differences in other phases were tested with 2×2 between-subjects ANOVA with incentive and rest/word-list learning as two factors in *Experiment 2*. Tukey honest significant difference (HSD) test was used in multiple post-hoc comparisons. Significance level was set at $p < 0.05$ in statistical tests. All data are reported as mean ± standard error (s.e.) across participants.

Results

Experiment 1

Baseline

In the baseline phase, the cursor was continuously displayed from the start of a trial to its moving beyond the invisible circle. The cursor's moving was congruent with the movement of the pen. No participants had difficulty following the instructions to carry out movements in this phase. In the last block of baseline (Fig. 2B), the reward group and the punishment group showed indistinguishable performance errors around 0° ($t(30)= 0.55$, $p= 0.58$, $d= 0.19$).

Adaptation

In the adaptation phase, the cursor was only displayed in the start square and its moving direction was rotated by 50° CCW relative to the movement of the pen. In the first adaptation trial, due to the suddenly added rotation and no previous experience, participants showed performance errors of approximately 50°. The mean performance error of the first adaptation trial in the reward group was 53.60° and that in the punishment group was 49.50°. An independent-samples t test showed no significant difference between the two groups ($t(30)= 1.73$, $p= 0.095$, $d= 0.61$). Participants were provided with reward or punishment feedback when the cursor moved through the invisible circular boundary. Since continuous feedback of the cursor was not provided, the planning of next action was based on incentive feedback from previous trials. Adaptation was assessed by the change of performance error.

Adaptation trials were blocked across 10 trials with a main effect of block on performance error indicating adaptation occurred. Fig. 2A shows performance errors across 30 blocks in the two experimental groups. A 2×30 mixed ANOVA was administered to examine differences of performance error in the two experimental groups. The ANOVA revealed a main effect of incentive (Fig. 2C, mean difference= 9.34°, $F(1,30)= 4.74$, $p= 0.037$, $\eta_p^2 = 0.14$) and a main effect of block (Greenhouse-Geisser adjustment: $F(3.80,114.13)= 23.18$, $p< 0.001$, $\eta_p^2 = 0.44$) but no significant interaction between incentive and block (Greenhouse-Geisser adjustment: $F(3.80,114.13)= 1.35$, $p= 0.26$, $\eta_p^2 = 0.04$). In the last block of adaptation, the reward and the punishment groups had comparable performance errors (Fig. 2D, t(30)= 1.03, p= 0.31, d= 0.36), indicating the total adaptation achieved in the two groups was similar.

Since continuous visual feedback of the cursor was not provided in the adaptation phase, participants had to plan the current reaching based on reward or punishment feedback from previous trials. If a participant received a small gain (reward: [0¢, +2¢)) or a big loss (punishment: [-5¢, -2¢]), the participant might make bigger change in adjusting the following reaching than when he/she received a big gain ([+2¢, +5¢]) or a small loss ((-2¢, 0¢]). Fig. 2H shows trial-by-trial change of performance error when participants received small gain or big gain and small loss or big loss. When participants received small gain or big loss, performance error change was negative, indicating performance error reduced, in both the reward and punishment groups, and the mean performance error change induced by big loss was

greater than that induced by small gain. When participants received big gain or small loss, performance error change was positive, indicating performance error increased, in both the reward and punishment groups, and the mean performance error change induced by small loss was smaller than that induced by big gain. A 2×2 ANOVA was administered to test the influence of incentive (punishment vs reward) and the magnitude of incentive (big vs small) on trial-by-trial change of performance error. The ANOVA showed a main effect of magnitude of incentive ($F(1,59)= 16.84$, $p< 0.001$, $\eta_p^2 = 0.22$) but no main effect of incentive ($F(1,59)= 2.30$, $p= 0.13$, $\eta_p^2 = 0.037$) and no significant interaction between incentive and magnitude ($F(1,59)= 0.0001$, $p= 0.99$, $\eta_p^2 = 0.00$).

Washout

In the washout phase, no rotation was applied to the cursor and continuous visual feedback of the cursor was provided. Participants on average showed limited after-effect, as revealed by performance errors in the first washout block in the two experimental groups (Fig. 2E). An independent-samples t test showed no significant difference of after-effect between the two groups ($t(30)= 0.77$, $p= 0.45$, $d= 0.27$). In the last block of washout (Fig. 2F), performance errors in the two groups drifted back around 0° and the group difference was not significant ($t(30)= 1.16$, $p= 0.25$, $d= 0.41$), indicating the washout was thorough in the two groups.

Re-adaptation

In the re-adaptation phase, the 50° CCW rotation was again added to the cursor movement. Fig. 2G shows performance errors in the first re-adaptation block in the reward group and the punishment group. An independent-samples t test revealed non-significant difference of performance errors between the two groups (t(30)= -1.84, p= 0.08, d= 0.65).

Savings

Savings was defined as the difference between exponential fitting parameter *b* in fitting the first 50 adaptation and re-adaptation trials (Morehead et al. 2015; Zarahn et al. 2008). A positive difference means re-adaptation was faster than adaptation, reflecting savings occurred in the re-adaptation phase. Fig. 2I shows savings in the punishment group and the reward group. An independent-samples t test showed non-significant difference in savings between the two groups (*t*(30)= 0.51, *p*= 0.62, d= 0.18).

In short, Experiment 1 provided participants with no continuous visual feedback of the cursor, so the adaptation was primarily driven by explicit process. In this context punishment induced significantly faster adaptation than reward but reward showed no advantage than punishment in consolidation measured as savings. The results indicate that the effects of reward and punishment may be influenced by the involvement of explicit and implicit processes underlying motor adaptation.

Experiment 2

Baseline

The baseline phase was the same as that in Experiment 1. No participants had difficulty following the instructions to carry out movements in this phase. In the last block of baseline (Fig. 3B), the four experimental groups showed indiscriminate performance errors around 0° ($F(3,36)= 1.16$, $p= 0.34$, $\eta_p^2 = 0.09$).

Adaptation

In the adaptation phase, continuous feedback of the cursor was provided and the moving direction of the cursor was rotated by 50° CW. The mean performance error of the first adaptation trial in each group was: the punishment-rest group 50.39°, the punishment-word group 42.87°, the reward-rest group 51.74°, and the reward-word group 51.66°. A two-way between-subjects ANOVA revealed no main effect of incentive ($F(1,36)= 2.72$, $p= 0.11$, $\eta_p^2 = 0.07$), no main effect of rest/word-list learning ($F(1,36)= 1.53$, $p= 0.23$, $\eta_p^2 = 0.04$), and no interaction ($F(1,36)= 1.47$, $P= 0.23$, $\eta_p^2 = 0.04$), indicating participants' first responses to the sudden rotation were similar. In each adaptation trial, participants were provided with reward or punishment feedback when the cursor moved beyond the invisible circular boundary. Fig. 3A shows performance error blocked across 10 trials in the four experimental groups. A three-way mixed ANOVA was administered to examine group differences in performance error in the adaptation phase. The ANOVA revealed a main effect of block (Greenhouse-Geisser adjustment: $F(3.48, 125.27)= 25.37$, $p< 0.001$, $\eta_p^2 =$

0.41), a main effect of incentive (Fig. 3C, mean difference= 8.26°, F(1,36)= 6.30, p= 0.017, $\eta_p^2 = 0.15$), but no main effect of rest/word-list learning (F(1,36)= 0.90, p= 0.35, $\eta_p^2 = 0.02$). The ANOVA also revealed no interaction between block and incentive (Greenhouse-Geisser adjustment: $F(3.48, 125.27) = 2.01$, $p = 0.11$, $\eta_p^2 = 0.05$), no interaction between block and rest/word-list learning (Greenhouse-Geisser adjustment: $F(3.48, 125.27) = 2.36$, $p = 0.07$, $\eta_p^2 = 0.06$), and no interaction among block, incentive, and rest/word-list learning (Greenhouse-Geisser adjustment: $F(3.48, 125.27) = 0.58$, $p = 0.66$, $\eta_p^2 = 0.016$). In the last block of adaptation, the four groups showed comparable performance error (Fig. 3D). A two-way between-subjects ANOVA revealed no main effect of incentive (F(1,36)= 0.15, p= 0.70, $\eta_p^2 = 0.004$), no main effect of rest/word-list learning (F(1,36)= 1.33, p= 0.26, $\eta_p^2 = 0.036$), and no interaction (F(1,36)= 0.24, P= 0.63, $\eta_p^2 = 0.007$), indicating participants' total adaptation was similar.

Trial-by-trial change of performance error was analyzed to assess how reward and punishment feedback influenced adaptation. If a participant received a small gain (reward: [0¢, +5¢)) or a big loss (punishment: [-12¢, -5¢]), the participant might make bigger change in adjusting the following reaching than when he/she received a big gain ([+5¢, +12¢]) or a small loss ((-5¢, 0¢]). Fig. 3G shows trial-by-trial change of performance error when participants received small gain or big gain and small loss or big loss. When participants received small gain or big loss, performance error change was negative, indicating performance error reduced, in both the reward and punishment groups, and the mean performance error change induced by big loss was

greater than that induced by small gain. When participants received big gain or small loss, performance error change was positive, indicating performance error increased, in both the reward and punishment groups, and the mean performance error change induced by small loss was smaller than that induced by big gain. A 2×2 ANOVA was administered to test the influence of incentive and the magnitude of incentive on trial-by-trial change of performance error. The ANOVA showed a main effect of magnitude of incentive ($F(1,76)= 54.42$, $p< 0.001$, $\eta_p^2 = 0.42$) and a main effect of incentive ($F(1,76)= 9.32$, $p= 0.003$, $\eta_p^2 = 0.11$) but no significant interaction between incentive and magnitude ($F(1,76)= 1.59$, $p= 0.21$, $\eta_p^2 = 0.02$).

De-adaptation

In the de-adaptation phase, rotation applied to the cursor was reversed to 50° CCW. Participants completed 15 de-adaptation trials. Fig. 3E shows performance errors of the first de-adaptation block in the four experimental groups. A 2×2 between-subjects ANOVA was administered to examine differences of performance error among the four groups. The ANOVA revealed a main effect of incentive (mean difference= -16.80°, $F(1,36)= 8.00$, $p= 0.008$, $\eta_p^2 = 0.18$) but no main effect of rest/word-list learning ($F(1,36)= 0.94$, $p= 0.34$, $\eta_p^2 = 0.025$) and no significant interaction between incentive and rest/word-list learning ($F(1,36)= 1.40$, $p= 0.24$, $\eta_p^2 = 0.037$).

Re-adaptation

In the re-adaptation phase, the 50° CW rotation was again added to the cursor movement. Fig. 3F shows performance error of the first re-adaptation block in the four experimental groups. A 2×2 between-subjects ANOVA showed no main effect of incentive ($F(1,36)= 2.97$, $p= 0.09$, $\eta_p^2 = 0.076$), no main effect of rest/word-list learning ($F(1,36)= 0.39$, $p= 0.54$, $\eta_p^2 = 0.01$), and no significant interaction between incentive and rest/word-list learning ($F(1,36)= 0.13$, $p= 0.72$, $\eta_p^2 = 0.004$).

Savings

Fig. 3H shows savings measured as the difference between exponential fitting parameter *b*. A positive difference means savings occurred. It was tested with a 2×2 between-subjects ANOVA, which showed a main effect of incentive ($F(1,36)= 6.76$, $p= 0.013$, $\eta_p^2 = 0.16$), main effect of rest/word-list learning ($F(1,36)= 4.50$, $p= 0.041$, $\eta_p^2 = 0.11$), and significant interaction between incentive and rest/word-list learning ($F(1,36)= 4.18$, $p= 0.048$, $\eta_p^2 = 0.10$). Simple effect analysis on the significant interaction revealed that there was significant difference between the Punishment-Rest group and the Reward-Rest group (mean difference= -0.57, $F(1,36)= 10.79$, $p= 0.002$, $\eta_p^2 = 0.23$) and also significant difference between the Punishment-Rest group and the Punishment-Word group (mean difference= -0.51, $F(1,36)= 8.68$, $p= 0.006$, $\eta_p^2 = 0.19$) but no significant difference between the Punishment-Word group and the Reward-Word group (mean difference= -0.068, $F(1,32)= 0.15$, $p= 0.70$, $\eta_p^2 = 0.004$) and no significant difference between the

Reward-Rest group and the Reward-Word group (mean difference= -0.009, $F(1,32)$= 0.003, p= 0.96, $\eta_p^2 = 0.00$).

Word-list learning

Immediately after the adaptation phase, one reward group and one punishment group learned a list of English words for five times. They completed the first free recall after 15-minute delay and the second free recall after a six-hour delay. Fig. 3I shows the number of correctly recalled words in the two free recall tests in the two groups. A 2×2 mixed ANOVA revealed no main effect of incentive ($F(1,18)$= 1.44, p= 0.24, $\eta_p^2 = 0.07$) but a trend for the effect of time ($F(1,18)$= 4.11, p= 0.058, $\eta_p^2 = 0.18$), and no significant interaction between incentive and time ($F(1,18)$= 0.31, p= 0.59, $\eta_p^2 = 0.017$).

Discussion

The purpose of the present study was to check the effects of monetary reward and punishment feedback, and to test the role of explicit process in the acquisition and consolidation of visuomotor adaptation memory. By controlling visual feedback of the cursor, the involvement of explicit process and implicit process in the visuomotor adaptation was controlled. As hypothesized, we found that, compared to reward, punishment induced faster adaptation when explicit process was primarily involved and when both explicit and implicit processes were involved. When the adaptation was driven by both explicit and implicit processes, punishment showed a disadvantage in offline consolidation of the visuomotor adaptation memory. This disadvantage in

offline consolidation caused by punishment was reduced by a word-list learning task immediately after the adaptation.

Punishment induced faster adaptation in both non-continuous and continuous visual feedback contexts

The present study provided further evidence that punishment, compared to reward, enhanced visuomotor adaptation in both experiments (Galea et al., 2015). In *Experiment 1*, the cursor was only displayed in the start square. Since there was no continuous visual feedback of the cursor, explicit process based on performance error dominated the visuomotor adaptation. This inference is based on the following findings. First, reward feedback alone produced no change in the predicted sensory consequences of motor commands and provided no sensory prediction error (Izawa & Shadmehr, 2011), which was also thought to drive implicit process (Taylor et al., 2014). Second, a latest study reported that direction information of errors was necessary in forming sensory prediction errors (Butcher & Taylor, 2017), but reward or punishment feedback in *Experiment 1* only provided magnitude information of errors. Moreover, we compared the size of after-effect in the present study to that in Mazzoni and Krakauer (2006), in which the rotation size was 45° and the wash-out amount was 60 trials. They reported average after-effect in the two experiment groups with 45° rotation and continuous visual feedback of the cursor in the adaptation phase (implicit process involved) were 14.4° and 16.5°, and the average after-effect in the third experiment group without rotation applied in the adaptation phase but using an explicit aiming cue

and strategy (pure explicit process was thought to be involved) was around 0° (estimation based on the figure published for specific datum was not reported). In the present study, the average after-effect across the first 60 wash-out trials in the punishment group was 1.55° and in the reward group was 1.36°. Based on this comparison, we infer that explicit process was primarily involved in *Experiment 1*.

In contrast, in *Experiment 2*, continuous visual feedback of the cursor was provided throughout the reaching. Sensory prediction errors were formed and implicit process from sensory prediction errors was involved. Meanwhile, participants were also provided with graded punishment or reward feedback based on performance error. Hence, in the context of continuous visual feedback of the cursor, the visuomotor adaptation was driven by explicit and implicit processes.

In both *Experiment 1* and *Experiment 2*, as was hypothesized, it was found that punishment induced significantly faster adaptation compared to reward. According to Galea et al. (2015), this could be due to punishment-increased sensitivity of the cerebellum to sensory prediction errors. While this explains the finding from *Experiment 2*, it does not explain the finding from *Experiment 1* for sensory prediction errors were not formed.

Another explanation is that punishment may drive participants to form more efficient explicit strategies compared to reward. This explains the findings from both *Experiment 1* and *Experiment 2*. In *Experiment 1*, the visuomotor adaptation was dominantly driven by explicit process and it showed that punishment induced faster

adaptation compared to reward, indicating participants in the punishment group formed more efficient explicit process. In *Experiment 2*, the visuomotor adaptation was driven by both explicit and implicit processes and it also showed that punishment induced faster adaptation. Faster adaptation induced by punishment could be realized by faster explicit process or faster implicit process. Considering the evidence that explicit process is flexible and implicit process is rigid and invariant (Bond & Taylor, 2015; Morehead et al., 2017), we thought that the faster adaptation induced by punishment in *Experiment 2* was the result of more efficient explicit process generated by punishment. This is supported by the results of trial-by-trial change of performance error after receiving small gain or big gain and small loss or big loss. In both *Experiment 1* and *Experiment 2*, it was found that receiving big loss or small gain decreased performce error and punished participants showed greater decreasing magnitude of trial-by-trial change of performance error after receiving big loss than rewarded participants after receiving small gain, indicating big loss induced greater exploration than small gain.

Punishment may be more effective than reward to disentangle incorrect strategies or aiming directions in early trials of adaptation and thus induce more efficient explicit process and faster adaptation. Wasserman and colleagues (2015) found that pruning of incorrect associations played a critical role in associative learning and reward attenuated this pruning. They trained pigeons to categorize photographic stimuli into categories under the influence of food reward or dark time-out punishment. A target stimulus was paired with a distractor stimulus in each trial and pigeons were cued to correctly select the stimulus that belonged to a category. They found that a distractor

stimulus that had been rewarded as a target in the previous trial reduced selection accuracy in the current trial, reflecting that pigeons had difficulty suppressing responses to previously rewarded stimuli. This is in accordance with design of the present study, in which imperfect hitting was rewarded or punished, with reward likely deferring participants to search for the optimal solution.

Reward enhanced offline consolidation of visuomotor adaptation memory in continuous visual feedback context

Experiment 2 showed that reward enhanced offline consolidation of visuomotor adaptation memory when continuous visual feedback of the cursor was provided (Abe et al., 2011; Wächter et al., 2009). Specifically, when they adapted to an opposite 50° CCW rotation (no incentive feedback provided) at 30 minutes after they adapted to a previous 50° CW rotation, the two reward groups adapted more slowly compared to the two punishment groups, indicating the two reward groups had stronger proactive interference from previous adaptation memory, which should be due to that reward enhanced offline consolidation of previous adaptation memory compared to punishment. Moreover, when adapted to the same 50° CW rotation after a six-hour delay, the two reward groups showed significantly greater savings than the punishment group that rested for 30 minutes, also showing that reward facilitated offline consolidation of previous adaptation memory compared to punishment. The benefit of reward on consolidation of visuomotor adaptation memory might be due to reward-induced fast neural plasticity in the primary motor cortex (Thabit et al., 2011).

Offline Consolidation of punishment-induced visuomotor adaptation memory was altered by the word-list learning task.

Experiment 2 showed that a word-list learning task immediately after the adaptation training altered the consolidation of punishment-induced adaptation memory. Firstly, thirty minutes after the adaptation training, punished participants that learned the word-list showed better performance in the de-adaptation phase adapting to an opposite rotation compared to punished participants that rested in the lab. Secondly, compared to punished participants that rested in the lab for 30 minutes, punished participants that learned the word-list had greater savings at six hours after the visuomotor adaptation training. However, rewarded participants that learned the word list or rested in the lab showed comparable de-adaptation performance and savings. These results suggest that punishment, compared to reward, induced stronger explicit component of visuomotor adaptation memory and competition from the stronger explicit motor memory component further inhibited offline consolidation of the adaptation memory (Brown & Robertson, 2007; Keisler & Shadmehr, 2010). To the punished participants that learned the word list, the word-list learning generated competitive declarative memory, which may suppress the explicit adaptation memory component formed through the visuomotor adaptation and further contribute to improvement in the six-hour delayed offline consolidation of the adaptation memory. In contrast, to the punished participants that rested in the lab for 30 minutes, competition from the stronger explicit motor memory component formed through the visuomotor adaptation inhibited the offline consolidation of the adaptation memory.

This is consistent with the hypothesis proposed by Brown and Robertson (2007). They thought that offline consolidation improvement of motor memory required disengagement of competition between explicit and implicit memory components.

The finding that the word-list learning altered consolidation of punishment-induced adaptation memory is also in accordance with the findings that punishment was associated with activation of dorsolateral prefrontal cortex (DLPFC) (Hester, Murphy, Brown, & Skilleter, 2010) and inhibitory TMS applied to DLPFC immediately after training changed offline consolidation of motor memories (Galea, Albert, Ditye, & Miall, 2010). The prefrontal cortex represents cognitive rules and plays a critical role in the initial phase of motor skill acquisition (for review see Frank, 2011).The reason that the word-list learning altered the consolidation of punishment-induced adaptation memory may be due to the overlapping neural underpings such as medial temporal lobe during both declarative and procedural learning (for review see Robertson, 2012).

That the punishment-rest group showed no savings may also likely be because this group stuck to the opposing de-adaptation strategy in its re-adaptation and thus slowered the re-adaptation rate. If this was so, there would be difference in the initial trials of the re-adaptation between the two punishment groups. However, the two punishment groups both showed comparable positive mean performance errors (same sign as adaptation error) in the first block of re-adatation trials. This reflects that the punishment-rest group may not stick to the opposing de-adaptation strategy that would slow down its re-adaptation.

Several limitations exist in the present study. First, explicit process was not directly measured and this constrained the capacity to assess the contribution of explicit and implicit processes during the adaptation. Although it is certain that explicit process was involved in both experiments, its contribution was not measured by either objective or subjective methods. Second, it was not tested how reward and punishment would influence the visuomotor adaptation that is dominantly implicit. Finally, although it is found in the present study that a word-list learning task altered the consolidation of punishment-induced visuomotor adaptation memory, it is not clear why declarative memory interfered with the explicit component of the visuomotor adaptation memory.

In summary, the present study demonstrates the distinct effects of reward and punishment on visuomotor adaptation and supports the possibility that the interaction between explicit process and implicit process plays a role in the dissociable effects of punishment and reward. Punishment induced more efficient explicit process than reward but also generated stronger competition between explicit and implicit motor memory components, which further inhibited offline consolidation of the punishment-induced visuomotor adaptation memory.

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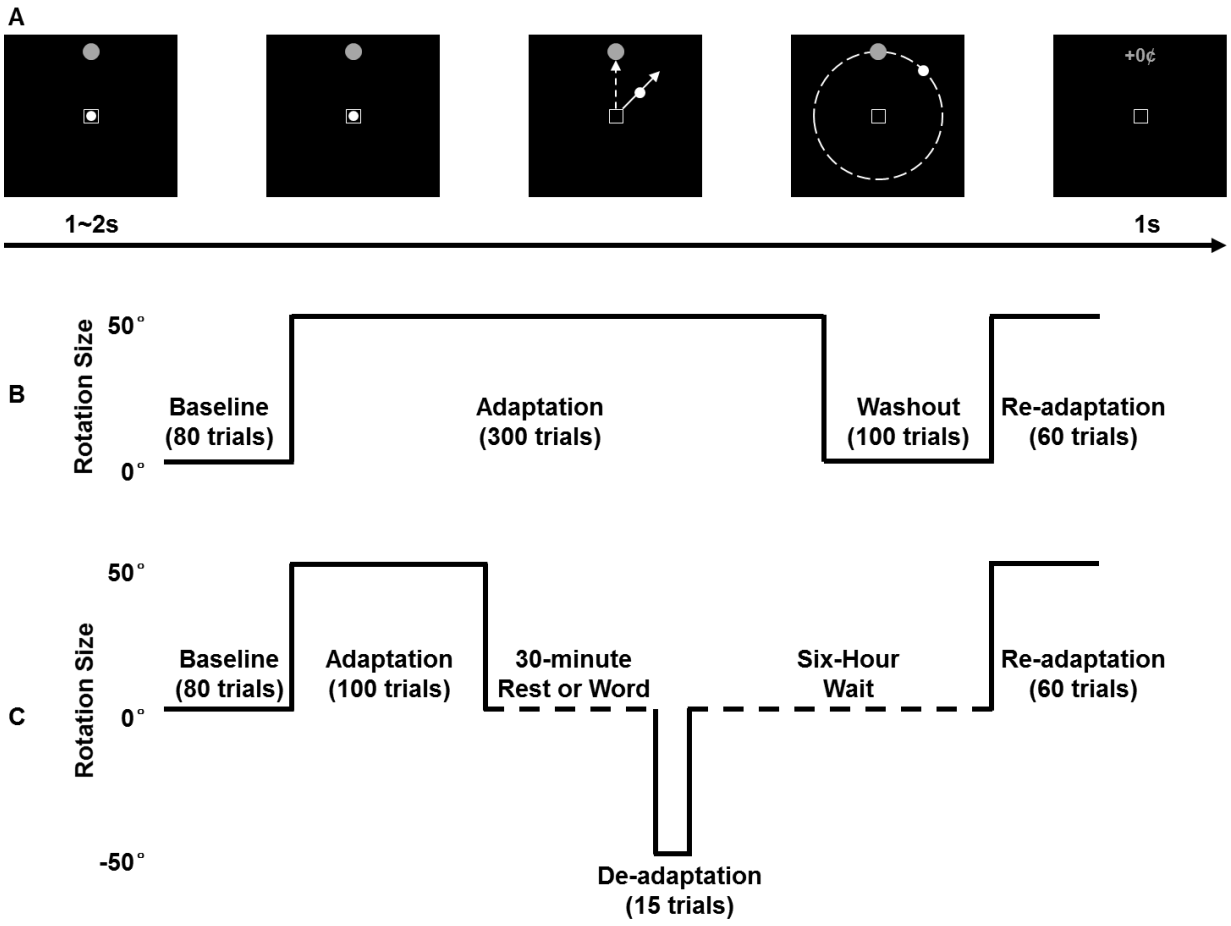

Fig. 1. A: experimental task schematic illustration: each frame shows the start square, the cursor (the white dot), the target (the grey dot, the target firstly appeared in red to inform movement preparation, then after 1~2s it changed into green to inform movement initiation), the invisible circular boundary (dashed circle, not displayed on the monitor), the heading direction of the cursor (solid arrow, Experiment 1 provided no visual feedback of the cursor outside the start square, Experiment 2 provided continuous visual feedback of the cursor, and in both experiments no visual feedback of the cursor was provided when the cursor moved outside the invisible circular boundary and when it moved back), and the heading direction of the hand (dashed arrow, direct vision of the hand was blocked), and monetary feedback (+0¢ in grey, actually displayed in red and 48 font size for 1s); B: test conditions in Experiment 1, rotation was 50° CCW; C: test conditions in Experiment 2, rotation was 50° CW and 50° CCW.

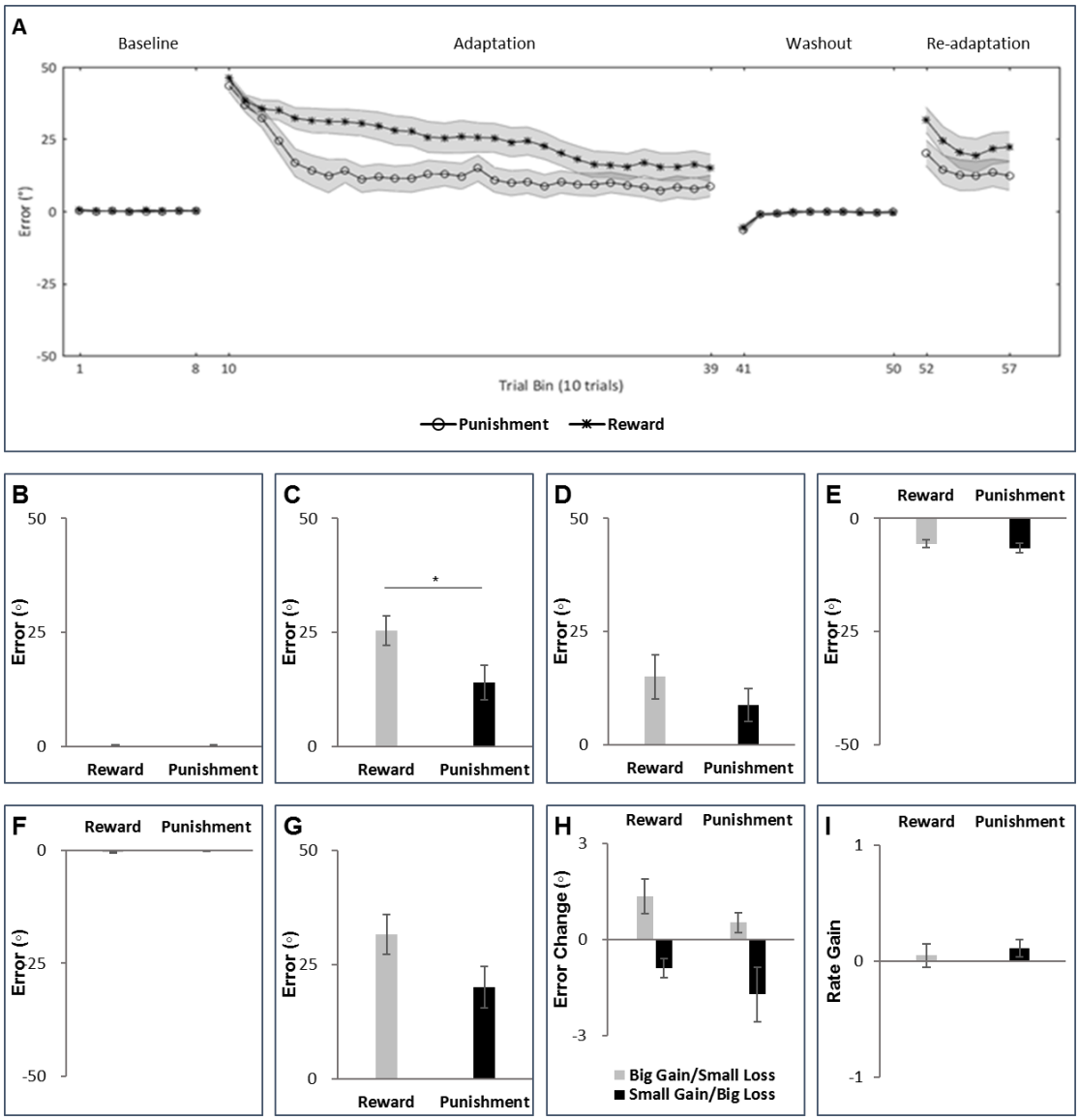

Fig. 2. Performance measures in Experiment 1. A: blocked mean performance error in each tasting phase, shaded area represents confidence interval around the mean; B: mean performance error of the last baseline block; C: mean performance error of the adaptation phase; D: mean performance error of the last adaptation block; E: mean performance error of the first washout block; F: mean performance error of the last washout block; G: mean performance error of the first re-adaptation block; H: Trial-by-trial change of performance error after receiving small gain or big gain and small loss or big loss (small gain: [0¢, +2¢), big gain: [+2¢, +5¢], big loss: [-5¢, -2¢], small loss: (-2¢, 0¢]; I: savings measured as gain of exponential fitting parameter *b* from the first 50 trials in the adaptation phase to the first 50 trials in the re-adaptation phase. * represents $p < 0.05$; ** represents $p < 0.01$, *** represents $p < 0.001$.

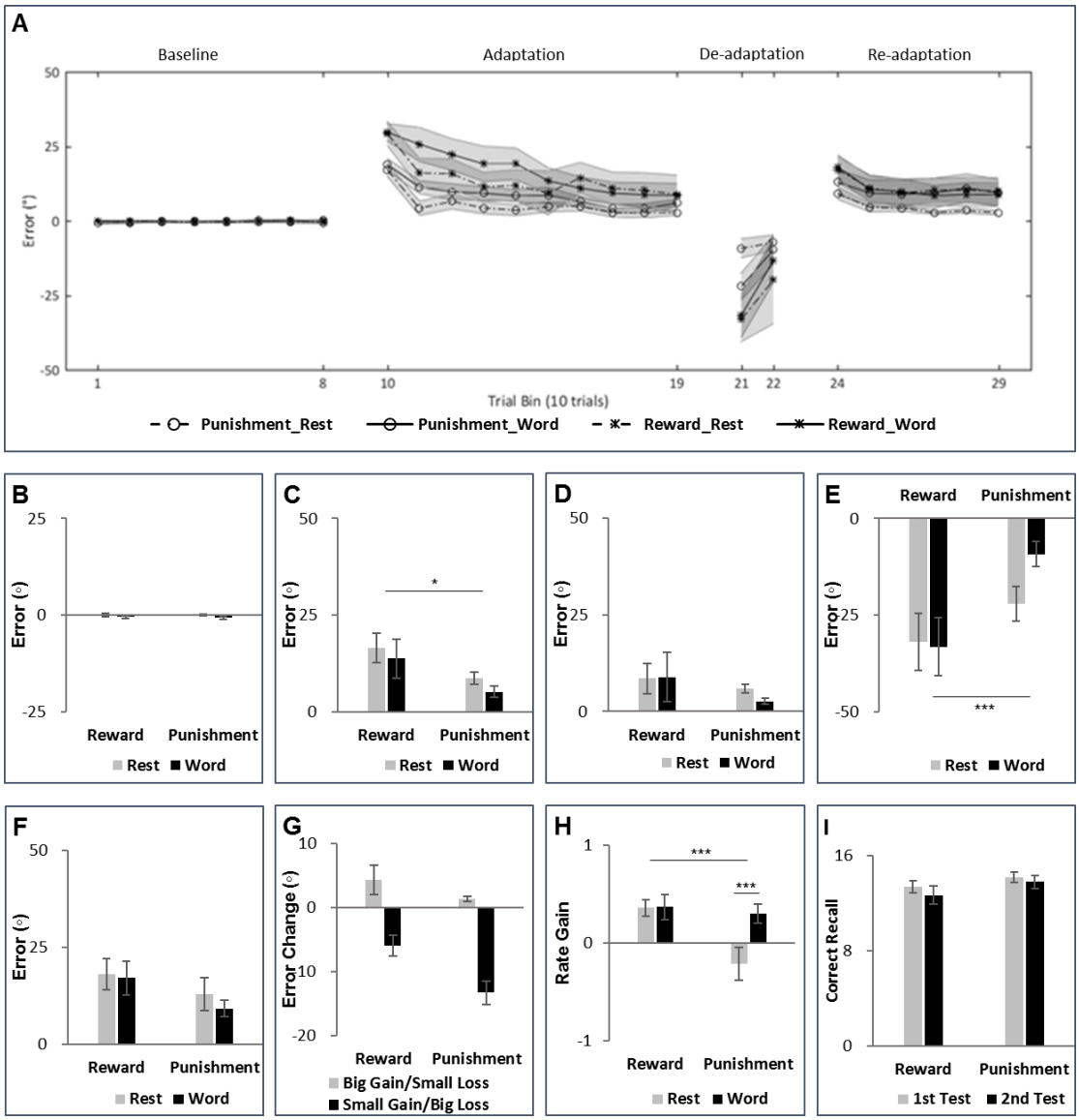

Fig. 3. Performance measures in Experiment 2. A: blocked mean performance error in each tasting phase, shaded area represents confidence interval around the mean; B: mean performance error of the last baseline block; C: mean performance error of the adaptation phase; D: mean performance error the last adaptation block; E: mean performance error of the first de-adaptation block; F: mean performance error of the first re-adaptation block; G: Trial-by-trial change of performance error after receiving small gain or big gain and small loss or big loss (small gain: [0¢, +2¢), big gain: [+2¢, +5¢], big loss: [-5¢, -2¢], small loss: (-2¢, 0¢]; H: savings measured as gain of exponential fitting parameter *b* from the first 50 trials in the adaptation phase to the first 50 trials in the re-adaptation phase; I: number of correctly recalled words in the first and second free recall. * represents $p < 0.05$; ** represents $p < 0.01$, *** represents $p < 0.001$.

Appendix – IRB approval

IOWA STATE UNIVERSITY
OF SCIENCE AND TECHNOLOGY

Institutional Review Board
Office for Responsible Research
Vice President for Research
1138 Lincoln Way, Suite 202
Ames, Iowa 50014
515 294-4566

Date: 1/18/2017

To: Yanlong Song
283 Forker

CC: Dr. Ann Smiley-Oyen
242 Forker Bldg

From: Office for Responsible Research

Title: Modulating Visuomotor Adaptation: The Effects of Reward and Penalty

IRB ID: 15-754

Approval Date:	1/18/2017	Date for Continuing Review:	1/18/2019
Submission Type:	Continuing Review / Modification	Review Type:	Expedited

The project referenced above has received approval from the Institutional Review Board (IRB) at Iowa State University according to the dates shown above. Please refer to the IRB ID number shown above in all correspondence regarding this study.

To ensure compliance with federal regulations (45 CFR 46 & 21 CFR 56), please be sure to:

- Use only the approved study materials in your research, including the recruitment materials and informed consent documents that have the IRB approval stamp.
- Retain signed informed consent documents for 3 years after the close of the study, when documented consent is required.
- Obtain IRB approval prior to implementing any changes to the study by submitting a Modification Form for Non-Exempt Research or Amendment for Personnel Changes form, as necessary.
- Immediately inform the IRB of (1) all serious and/or unexpected adverse experiences involving risks to subjects or others; and (2) any other unanticipated problems involving risks to subjects or others.
- Stop all research activity if IRB approval lapses, unless continuation is necessary to prevent harm to research participants. Research activity can resume once IRB approval is reestablished.
- Complete a new continuing review form at least three to four weeks prior to the date for continuing review as noted above to provide sufficient time for the IRB to review and approve continuation of the study. We will send a courtesy reminder as this date approaches.

Please be aware that IRB approval means that you have met the requirements of federal regulations and ISU policies governing human subjects research. Approval from other entities may also be needed. For example, access to data from private records (e.g. student, medical, or employment records, etc.) that are protected by FERPA, HIPAA, or other confidentiality policies requires permission from the holders of those records. Similarly, for research conducted in institutions other than ISU (e.g., schools, other colleges or universities, medical facilities, companies, etc.), investigators must obtain permission from the institution(s) as required by their policies. IRB approval in no way implies or guarantees that permission from these other entities will be granted.

Upon completion of the project, please submit a Project Closure Form to the Office for Responsible Research, 202 Kingland, to officially close the project.

Please don't hesitate to contact us if you have questions or concerns at 515-294-4566 or IRB@iastate.edu.

CHAPTER 5. CONCLUSION

Motor adaptation was traditionally thought as an implicit process that was driven by sensory prediction error, which is the difference between the predicted sensory consequence and the actual sensory feedback. These studies demonstrated that adaptation to an abrupt visual rotation could also be driven by motivational feedback, with reward and punishment showing distinct effects on the adaptation process as well as the consolidation of the visuomotor adaptation memory.

These studies demonstrated that young healthy participants could adapt to a 50° visual rotation when only provided with performance-based reward or punishment feedback. Without continuous visual feedback of the cursor, sensory prediction error could not be formed, and the adaptation was primarily an explicit process driven by motivational feedback from the reward or punishment participants received. When continuous visual feedback of the cursor was provided and motivational feedback was distributed, the adaptation was driven by the interplay between explicit and implicit processes. Thus, both sensory feedback and motivational feedback were shown to drive visuomotor adaptation.

The three experiments all demonstrated that punishment, compared to reward, induced faster visuomotor adaptation to an abrupt visual rotation, supporting the robust enhancing effect of punishment on visuomotor adaptation. This enhancing effect of punishment was probably due to punished participants forming a more efficient explicit strategy or explicit process in the adaptation phase. There are several

lines of evidence that support this conclusion. First, the present study applied an abrupt 50° visual rotation of the cursor. All participants were very surprised at the beginning when the rotation was applied. This abrupt rotation elicited participants' explicit exploration of ways to counterbalance the rotation, making the adaptation involve explicit learning. The explicit exploration was reflected by trial-by-trial change in performance error. Second, in the context of a lack of continuous visual feedback of the cursor, the adaptation was also driven by explicit learning and punished participants induced faster adaptation compared to rewarded participants. Third, in the context of continuous visual feedback of the cursor, the adaptation was driven by both explicit and implicit processes, with punished participants also exhibiting faster adaptation. Last, in all three experiments, it was found that punished participants had greater trial-by-trial decrease of performance error when they received a big loss compared to rewarded participants when they received a small gain. This indicates that punished participants showed faster exploration to search for the optimal method to counterbalance the abrupt rotation to minimize loss, likely due to loss aversion. This was also supported by the finding that punished participants had smaller trial-by-trial change of performance error when they received small loss than rewarded participants when they received big gain, indicating punished participants showed less variability in their movements than rewarded participants. In brief, all these findings support the position that punishment, compared to reward, induced more efficient explicit learning and thus drove faster adaptation to the abrupt rotation.

A second overall finding was that the involvement of explicit process in the adaptation phase modulated the impact of reward and punishment on the consolidation of visuomotor adaptation memory. In the context of non-continuous visual feedback of the cursor in which adaptation was driven by explicit learning, offline consolidation of punishment-induced adaptation memory and reward-induced adaptation memory were comparable. However, in the context of continuous visual feedback of the cursor in which the adaptation was driven by both explicit learning and implicit learning, offline consolidation of punishment-induced adaptation memory, compared to that of reward-induced adaptation memory, was inhibited. This inhibition was likely the result of stronger explicit adaptation memory formed by punishment-induced adaptation. Stronger explicit adaptation memory may compete with implicit adaptation memory and constrain the consolidation and expression of punishment-induced visuomotor adaptation memory. This was supported by the finding that punishment had evident offline consolidation improvement expressed as savings when punishment was randomly distributed in only 50% of adaptation trials than when punishment was distributed in 100% of adaptation trials. The magnitude of trial-by-trial change of performance error was smaller when participants received big punishment in 50% of adaptation trials than in 100% of adaptation trials, indicating the explicit exploration was slower in the 50% condition and thus weaker explicit memory. Hence the offline consolidation of 50%-punishment-induced adaptation was not inhibited. The other evidence that strong explicit adaptation memory inhibited offline consolidation of adaptation memory was from the finding that an explicit

word-list learning task immediately after the adaptation training enhanced the offline consolidation of punishment-induced adaptation memory but had no influence on the offline consolidation of reward-induced adaptation memory, reflecting that punishment had stronger explicit adaptation memory than reward. These findings support that punishment induced more efficient explicit learning and faster adaptation but also stronger explicit adaptation memory, which inhibited the offline consolidation of punishment-induced adaptation memory.

In summary, this study provided further evidence that punishment accelerated acquisition of motor memory and reward enhanced consolidation of motor memory. The distinct effects of punishment and reward are likely due to an explicit process difference. This study demonstrated the influence of explicit process in motor adaptation and showed the competitive nature of explicit and implicit components in consolidation of motor memory.

Several limitations exist in the present study. First, explicit process was not directly measured, and this constrained the capacity to assess the contribution of explicit process and implicit process during the adaptation process. Although it is certain that explicit process was involved in all three experiments, its contribution was not measured by either objective or subjective methods. Second, it was not tested how reward and punishment would influence the visuomotor adaptation that is dominantly implicit. Based on the evidence that implicit process is rigid, it is likely that reward and punishment would induce comparable visuomotor adaptation and consolidation of

visuomotor adaptation memory. Finally, although it is found in the present study that a word-list learning task altered the consolidation of punishment-induced visuomotor adaptation memory, it is not clear why declarative memory interfered with the explicit component of the visuomotor adaptation memory. This interference questions the nature of motor memory and the interaction between declarative memory and motor memory. How multiple processes and multiple memory systems interact to influence motor learning is a question worthy of further investigation.

Movements play fundamental roles in human daily living and greatly affect the quality of life. However, the acquisition of many movement skills requires long-term practice, and many factors such as disease and environmental change may impair the acquired movement skills. Many approaches and factors have been explored to modulate the acquisition and consolidation of motor memories. This study further demonstrated the effects of reward and punishment on acquisition and consolidation of motor adaptation memories. Findings from this study are also of potential practical importance in benefitting real applications such as sports training and rehabilitation services. For instance, findings on the benefit of reward in consolidating motor memories may entail the introduction of reward (such as praise) rather than punishment (yelling or removal from the game, or other forms of disapproval) in training protocols. Likewise, findings on the influence of probability of incentive distribution may further guide the design of incentive delivery protocol in real scenarios.